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HEREDITAS

GENETISKT ARKIV

UTGIVET AV MENDELSKA SÄLLSKAPET I LUND

REDAKTÖR: ROBERT LARSSON

BAND XXVII HÄFT. 3—4

LUND 1941, BERLINGSKA BOKTRYCKERIET

HEREDITAS,

a periodical devoted to the publication of original research in heredity, is published by the MENDELIAN SOCIETY at Lund, Sweden. All contributions are written in English, German or French, illustrated, when necessary, with adequate text figures and plates. Each volume contains about 400 pages, issued in four numbers.

Subscriptions should be sent to the Editor. Price *Twenty-five (25) Swedish Kronor per volume.* Post free. (The price of Vols. I—X is 10 Swedish Kronor per volume, of Vols. XI—XXIII, 15 Sw. Kr., and of Vols. XXIV—XXV, 20 Sw. Kr.)

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THE CYTOLOGICAL EFFECT OF DIFFERENT SEED-TREATMENTS IN X-RAYED BARLEY

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IN recent papers on the cytogenetic effect of X-radiation it has been shown that the effect of the X-rays is directly influenced by the physiological condition of the cell and the nucleus. In meiosis and in microspores the active (reproducing) stages are much more sensitive to X-rays than the resting stages. The same thing also applies to somatic tissue. In dormant seeds all cells and nuclei are resting, and a variation of the nuclear status will immediately be revealed in an increased number of cytological disturbances at the same X-ray dosage.

The material for this investigation is the same as that used by GUSTAFSSON (1940) in his genetical analysis. In the present paper we shall deal exclusively with the Golden Barley series 1939: I: 21—24, irradiated with 10000 r (voltage 160 kv., 7,5 ma., 4 Al., 72 r/min.). The pre-treatments were as follows: I: 21, the seeds contained 10 % H_2O; I: 24, 15 % H_2O; I: 22, the seeds were treated with distilled water for 23 hours previous to the X-raying in order to induce germination; I: 23, the seeds were treated with 0,01 % of a hetero-auxin solution for 23 hours for the purpose of still further enhancing germination.

After irradiation the seeds were germinated and as soon as the roots had ruptured the coleorhiza, the radicles were fixed in Navashin's solution. The sections were 17 μ in thickness and were stained in gentian violet.

The cytological disturbances were of the usual type, chromosome fragments and bridges (two centromere formations), as has been described and figured in numerous papers. The fragments may vary very much in appearance, size and number, but are probably for the most part chromosome fragments (double).

In the present investigation longitudinal sections were exclusively used, and disturbed or undisturbed cells were determined at the anaphase or telophase stage. As it was probable, according to GUSTAFSSON (1937), that the frequency of disturbances varied in different tissues of the root, the determinations were made partly for the periblem and the dermatogen, partly for the plerome. The periblem

and the dermatogen were combined, as it was found that the boundary between them was too ill-defined to permit a careful classification. In the examination all analysable cells were determined per root. The column headed »fragments» in the tables gives the number of cells showing one or more fragments per cell. The same thing applies to the column headed »bridges».

As seen from Table 3, Series I: 21 with 10 % water content and Series I: 24 with 15 % water content show 12,66 % and 27,99 % disturbances respectively. An increase in the water content of the seeds by 5 % thus doubled the number of disturbances at the same X-ray dosage. In Series I: 22 (23 hours in H_2O) and Series I: 23 (23 hours in auxin) the number of disturbances rose to 53,80 % and 50,99 % respectively. The difference between these two values is not statistically significant. In the latter two cases the increase of disturbances was 4 times that in Series I: 21. Thus hetero-auxin does not seem to have any special effect, and the high frequency of disturbances must be attributed entirely to the water soaking, as in the case of Series I: 22. The two series may therefore be combined and this has been done in plotting the curve shown in Fig. 1.

The experiments prove conclusively that hydration is the primary cause of the increased lability of the nucleus. It has been known for quite a long time that a relatively slight increase in the water content brings about a great increase of respiration in resting seeds. This is in all probability followed by an increase in the activity of other living processes. KOLKWITZ (1901) gives the following values of carbon dioxide given out by 1 kilo of barley during 24 hours at a temperature of 18° C.:

11	%	water	content	0,35	mg.	CO_2
14—15	»	»	»	1,4	»	»
19,6	»	»	»	123,00	»	»
20,5	»	»	»	359,00	»	»
30,0	»	»	»	2000,00	»	»

The values for the classes of most interest to us, viz. those having 11 % and 14—15 % water content, show that respiration was increased by as much as four times in the latter class, from which we may draw the conclusion that metabolism in other respects had also greatly increased in intensity.

As already mentioned in the introduction, GUSTAFSSON (1937) has shown that in desiccated seeds (the B Series with 10 % water content)

the distribution of disturbances is irregular and that »the extreme cell layers of desiccated radicles are not so sensitive to X-raying as the cell layers in the middle of the radicles» (p. 308). The results obtained and the percentages of disturbed cells computed for the plerome and the periblem + dermatogen for each of the four series are presented in Table 1. As seen from the percentage figures the plerome showed in all cases a somewhat higher frequency of disturbances than the periblem + dermatogen, but the difference is not significant ($M = -1{,}68 \pm 1{,}30$), therefore there is no reason for assuming an irregular distribution of the disturbed cells in the present material.

TABLE 1. *Percentages of disturbed cells.*

Series	Number of roots		Number of normal cells	Number of disturbed cells	Number of analysed cells	% disturbed cells
1939: I: 21	15	Plerome	897	143	1040	13,75
		Periblem + dermatogen	724	92	816	11,27
I: 24	18	Plerome	721	295	1016	29,04
		Periblem + dermatogen	694	255	949	26,87
I: 22	12	Plerome	190	228	418	54,55
		Periblem + dermatogen	290	331	621	53,30
I: 23	10	Plerome	198	208	406	51,23
		Periblem + dermatogen	344	356	700	50,86

It should be noted that GUSTAFSSON determined the frequency of disturbances in the two outermost sections and compared the values with those obtained from the rest of the root. If it had been possible in the present material to estimate the frequency of disturbances in the dermatogen, it is conceivable that an irregularity in the distribution of disturbed cells would have been revealed in Series I: 21 (10 % water content). GUSTAFSSON considers this difference in frequency in dry seeds (the B Series with 10 % water content) to be due to the fact that the supply of water in the radicles is deposited in layers so that the peripheral cell layers have a lower water content than those situated in the centre. This would also be associated with an increased sensitivity to X-radiation in the inner cell layers. In the A Series (15 % water content) GUSTAFSSON was unable to show this irregularity.

Exceedingly great variations in the percentages of disturbed cells occurred in both Series I: 22 and Series I: 23. Since, as already shown, there is no reason for assuming an irregular distribution of the disturbed cells in the root-tip, such cells being randomly distributed instead, we are justified in combining the values obtained for the plerome and for the periblem + dermatogen. From this it is clear that the great variations in the percentages are directly associated with the number of observed divisions per root. In a few divisions per root

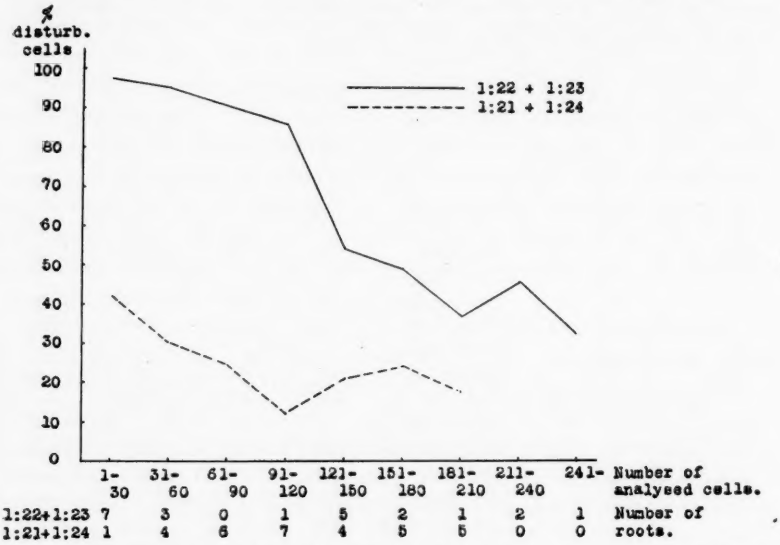


Fig. 1. The percentage of disturbed cells in relation to the frequency of divisions per root.

the number of disturbed cells will be maximal (100 %). If the frequency of divisions is increased the percentage of disturbed cells will fall and the mean percentage for both series will be about 52. If Series I: 22 and I: 23 (see p. 211) and Series I: 21 and I: 24 are combined, the soaked and the dry seeds are compared with each other. Now if a graph is plotted to show the percentage of disturbed cells in proportion to the number of divisions per root, we shall obtain curves having the appearance of those presented in Fig. 1. As it generally happened that several root-tips belonged to the same class, the mean percentage of the total number of disturbances has been recorded.

The curves run an entirely different course and are of a quite

different nature. For the soaked series R is equal to $-10{,}3123 \pm 2{,}849$ and for the dry series $R = -1{,}8703 \pm 1{,}035$. Thus for each class of 30 divisions the frequency of disturbed cells falls by 10,31 % in the soaked series and by 1,87 % in the dry series.

It is possible that the highest point in the »dry» curve (42,1 %) is somewhat misleading owing to the fact that only one root with 19 analysed divisions could be studied in the range 1—30. If we examine the conditions in the soaked series we shall find that 7 roots containing 1—8 divisions show 100 % disturbed cells and 1 root with 11 divisions has 90,9 % such cells. Although GUSTAFSSON employed another basis of calculation in his classification his values can no doubt be compared with those presented here. He determined the frequency of disturbances in 7—8 sections taken from the centre of the radicle. The percentage of disturbed cells is given per section. The following values are quoted from GUSTAFSSON's paper: »Within the range 0—5 divisions per section there are 2 radicles with 0,5 and 1 division per section respectively having 100 % disturbances, 3 radicles with 2, 2 and 2,8 divisions per section respectively possessing 89,8 %, 83,3 % and 50 % disturbances». The cases cited include both soaked and dry seeds. Analogous to the examples given here from the soaked series and from GUSTAFSSON's paper we are possibly justified in assuming that if Series I: 21 and I: 24 had contained roots with a maximal number of 10 analysable divisions per root they would have shown 100 % disturbed cells. The curve for the dry series would thus have shown a greater fall between the 1—30 and 31—60 classes than that revealed by the available values.

From the above it is quite evident that the cells that first enter into division show the highest frequency of disturbances. As the effect of X-rays is directly influenced by the physiological condition of the seeds it seems to be probable from the conditions described that there is a physiological variation between the individual cells of the seed. A seed is intrinsically a complicated formation, and it is hardly probable that complete homogeneity exists between its thousands of cells. The water content may be higher in one cell than in another, and in that way metabolism will also vary and cells with a lower water content will be in a more marked resting stage than those with a higher water content. At the same time as the resting stage gradually comes to an end and the living processes are intensified, the more or less gradual process of reproducing genes, chromosomes and fibrils begins. The cells (the nuclei) will thus be at different stages of development and

will show more or less sensitivity to X-rays. The cells that have started their reproduction earliest will also on an average be the first to divide at germination and at the same time show the highest frequency of disturbances.

If the percentage of cells with fragments and the percentage of cells with bridges are computed in proportion to the total number of analysed cases, we shall obtain two numerical series showing good proportionality. As seen from Table 2, approximately the ratio is 1 : 2 : 4 : 4. Further, if the percentage of cells with bridges is calculated in proportion to the number of disturbed cells very divergent figures are obtained (the greatest difference is 9,6). It nevertheless appears as if the frequency of bridges was rather constant and amounted to one-third the number of disturbed cells.

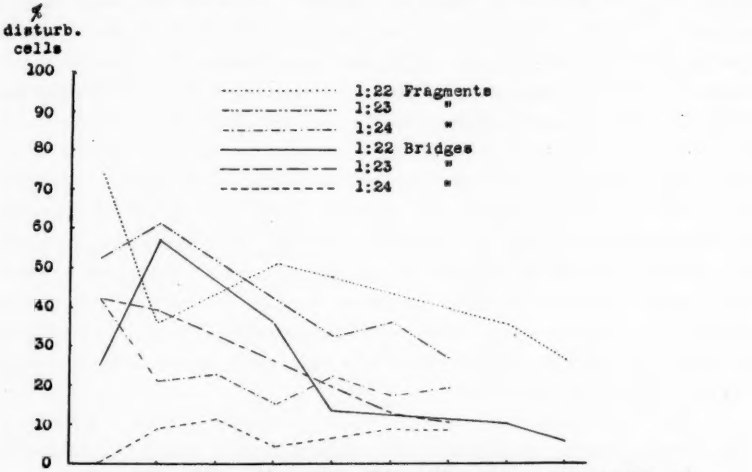
TABLE 2. *Cells with fragments and bridges.*

Series	Number of roots	Number of analysed cells	Number of cells with fragments	% fragments of Σ total	Number of cells with bridges	% bridges of Σ total	% bridges of disturbed cells
1939: I: 21	15	1856	145	7,81	90	4,85	38,29
I: 24	18	1965	392	19,95	158	8,04	28,73
I: 22	12	1039	389	37,44	170	16,36	30,41
I: 23	10	1106	375	33,91	189	17,09	33,51

In an analysis of the disturbances in ageing seeds following X-ray treatment GUSTAFSSON (1937, Table 17) found a proportional increase between fusions and fragments. On the other hand, he was unable to find such a proportionality in seeds having different water content. In the present investigation, however, it may be regarded as proved that in an increase of the water content from 10 to 15 % and in seeds soaked for 23 hours *the disturbances increase in proportion* after the same X-ray dosage, *and that the proportionality applies to the two different categories of disturbances.*

Since, as already shown, the earliest divisions exhibit the highest percentages of disturbed cells, it is conceivable that a change in the ratio of bridges to fragments may also take place in the lowest classes. GUSTAFSSON (1937) also considers that he was able to prove such a variation: »While fusion occurs chiefly in the classes with or immediately after a minimum rate of division (class 20—30), fragmentation takes place in all classes, but the proportion of fragments

to fusions increases considerably in the 0—20 class and in the 40—70 classes» (l. c. p. 325). If we examine the situation in Series I: 24, I: 22 and I: 23 (representative of the lower classes) we shall find that the proportion of bridges to fragments is, generally speaking, the same in all classes. From the graph (Fig. 2) it will be seen that the only evident deviation is shown by the 31—60 class in Series I: 22. Here the ratio of bridges to fragments has been reversed, 56,1 % bridges as against 36,6 % fragments being recorded. The curves for the other



	1-30	31-60	61-90	91-120	121-150	151-180	181-210	211-240	241-	Number of analysed cells.
1:22	5	2	0	1	1	0	0	2	1	Number of
1:23	2	1	0	0	4	2	1	0	0	roots.
1:24	1	4	3	2	2	4	2	0	0	

Fig. 2. The proportion of cells with fragments to cells with bridges in relation to the frequency of divisions.

two series run rather uniformly, therefore the above-mentioned deviation is probably to be regarded as a mere chance.

The results of the present investigation as well as those of earlier investigations by ERDMANN (1936), GUSTAFSSON (1937, 1940), KAPLAN (1939), and MARQUARDT and ERNST (1940) have conclusively proved that an increase of the water content of the cell brings about an increased sensitivity to X-rays. GUSTAFSSON and the present writer have investigated the conditions in seeds, ERDMANN has examined yeast-fungi, while SAX (1940), MARQUARDT and ERNST and KAPLAN have studied the effect of X-rays on microspores. In all these studies the

principle is the same, we have to do with either resting or dividing nuclei.

In his paper of 1939 KAPLAN has shown that swollen (water-treated for 8 hours) pollen grains of *Antirrhinum majus* after irradiation and fertilisation on normal ovules give the highest number of »F_1 Abweicher». On the other hand, if the period of water treatment is increased to 33 hours a smaller number of »F_1 Abweicher» is obtained. This is due, according to KAPLAN, to changes brought about by the longer period of swelling, which lead to a decrease in the frequency of disturbances, and in this connexion he refers to the chromosome doubling (p. 578). KAPLAN's view seems to be quite correct, and the stabilisation of the chromosomes demonstrated by the longer period of swelling can hardly be explained in any other way than that the sensitive reproductive stage is wholly or partly over. GUSTAFSSON (1937) has given expression to the same opinion, viz. that »X-raying in various stages of nuclear divisions has presumably its most injurious effect at the moment when the chromosomes are being reproduced. In their capacity of compound bodies, the chromosomes must show themselves most sensitive to external influences at the moment when the genes definitively give rise to daughter genes and the fibrils to daughter fibrils or when each gene or fibril gives rise to two new genes or fibrils» (l. c. p. 302).

After irradiation of mature and immature pollen grains of *Antirrhinum majus* MARQUARDT and ERNST (1940) found the following percentages of »F_1 Abweicher»: 12,16 % after treatment of immature pollen grains, 1,94 % after treatment of mature pollen grains. The resistence thus found in the mature pollen grains cannot be explained in any other way than by assuming a loss of water during the maturing period (l. c. p. 210).

In the pollen mitosis of *Tradescantia* (SAX, 1940) the greatest number of disturbances following X-radiation was found at prophase. The lability of prophase as compared with that of the resting stage is considered by SAX to be due to the following reasons (p. 61): »There are twice as many threads to be hit at prophase; terminal deletions can be produced at prophase by lateral fusion between broken chromatids while in the resting stage they are produced only when the broken end loses its capacity for fusion; and the secondary factors of chromosome torsion and movement would be expected to be greater at prophase».

The primary cause of the lability which, according to SAX, char-

acterizes prophase is, we presume, the hydration that the nucleus must probably pass through in order to be able to enter into a dividing stage. Thus in this case, too, the increased water content would be the primary cause of the increase of disturbances.

From a colloidochemical as well as a radiophysical point of view it appears probable that the concentration of intermicellar water is the cause of the increased lability of the chromosomes and the molecules. MARQUARDT and ERNST (1940) also cite the following: »Der Verlust des freien, intermicellaren und nicht durch elektrische Kräfte an die Kolloidteilchen gebundenen Wassers bringt eine starke Erhöhung der Reaktionswiderstände aller Umsetzungen, vor allem der Enzymreaktionen mit sich» (p. 209—210). Breakages of chromosomes may occur by shattering the molecular complex under the influence

TABLE 3. *Sterility and mutation frequency.*

Series	% disturbed cells	% sterility of X_1 plants	% mutations of X_2 plants	% disturbed cells/ % mutations
1939: I: 21	12,66	51,61	7,89	12,66 : 7,89 = 1,60
I: 24	27,99	76,73	13,45	27,99 : 13,45 = 2,08
I: 22	53,80	87,61	26,21	53,80 : 26,21 = 2,05
I: 23	50,99	90,29	31,86	50,99 : 31,86 = 1,60

of the energy of the X-rays. This effect takes place most easily at some point where the union between the different atoms is relatively weak, or (and) where the action may be thought to be intensified by the resonance phenomena. It is not likely that water produces a disturbing frequency influence by itself, as there is no characteristic fluorescent X-radiation in elements (H and O) with such low atomic numbers. In this case it is therefore probable that the increased sensitivity to a higher degree of humidity is produced by the water penetrating in some way or other into or being added to the protein molecules, thereby weaking their internal union. This need not imply a chemical combination between protein and water, the influence being of a purely physical nature. The high dipole moment of water may possibly render it especially active in this respect.

The genetic analysis of the present material (GUSTAFSSON, 1940) shows that both the sterility and the mutation frequency in the X_1—X_2 plants increase with an increased water content following radiation with the same X-ray dosage. Table 3 gives GUSTAFSSON's values (1940,

p. 5, Table 1) together with the percentages of disturbed cells found in the present investigation. As appears from the table all three phenomena show a marked parallelism. The most evident feature perhaps is that the same proportionality existing between the percentage of disturbed cells in the different series is also found in the percentage of mutations, viz. approximately 1 : 2 : 4 : 4. Moreover, it will be seen that the values for Series I: 22 and I: 23 do not show greater differences than may be expected to fall within the limits of error and consequently, as already pointed out, there is no difference in the effect of a 23 h. water treatment and a 23 h. auxin treatment.

GUSTAFSSON is of opinion that »sterility and mutation rate imply connected phenomena» (1940, p. 7). The parallelism demonstrated here between the different phenomena justify us in laying down the following rule: *If the physiological condition within the seed has been changed so that an increase in the number of disturbed cells takes place after the same X-ray dosage we may expect an increase partly in the percentage of sterility of the X_1 generation, partly in the frequency of mutations in the X_2 generation. If the percentage of disturbed cells is twofold the mutation frequency will also be doubled.*

For valuable assistance in the statistical treatment of the material I beg to express my gratitude to Dr. O. TEDIN, Svalöf. I also wish to thank Prof. T. GUSTAFSSON and Dr. A. HERRLIN, Lund, for discussions on radiophysical problems.

SUMMARY.

1. After X-raying with the same dosage (10000 r) the reaction of the chromosomes is directly influenced by the physiological condition of the seeds. Seeds containing 10 % water show 12,66 % disturbed divisions, seeds with 15 % water 27,99 %, and seeds soaked 23 hours in water or in 0,01 % hetero-auxin solution 53,80 and 50,99 % disturbances respectively.

2. The disturbed cells show probably a random distribution in different parts of the roots.

3. The cells that first enter into division show the highest frequency of disturbances.

4. If the percentage of cells with fragments and the percentage of cells with bridges are computed in proportion to the total number of analysed cases, we obtain two numerical series showing good

proportionality, approximately the ratio is 1 : 2 : 4 : 4. The frequency of bridges seems to be $^1/_3$ of the disturbed cells.

5. The proportion of bridges and fragments is, generally speaking, the same in all division classes.

6. There is a marked parallelism between the percentages of disturbed cells, sterility and mutation rate. The most evident feature is that the same proportionality existing between the percentages of disturbed cells in the different series is also found in the percentage of mutations, viz. approximately 1 : 2 : 4 : 4.

7. The parallelism demonstrated here between the different phenomena justify us in laying down the following rule: If the physiological condition within the seed has been changed so that an increase in the number of disturbed cells takes place after the same X-ray dosage we may expect an increase partly in the percentage of sterility of the X_1 generation, partly in the frequency of mutations in the X_2 generation. If the percentage of disturbed cells is twofold the mutation frequency will also be doubled.

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COLCHICINE-INDUCED TETRAPLOIDY IN SEQUOIA GIGANTEA

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THE colchicine method for the production of polyploids has now been available for nearly three years, and during this time a great many plants of different systematic position have been tested with colchicine. In the Angiosperm class representatives of about 30 families have been studied, and their cytological reaction to colchicine seems to be identical (see the surveys in GYÖRFFY, 1940, and LEVAN, 1940 b), if the special immunity of *Colchicum* is not taken into account (LEVAN, 1940 a). In the Gymnosperms, on the other hand, the situation is so far almost unknown. Only one communication has appeared dealing with the induction of polyploidy in somatic tissues of *Pinus* (MIROV and STOCKWELL, 1939). It therefore seems to be justified in the present paper to describe some results of colchicine treatments in *Sequoia gigantea*, although, of course, the tetraploids produced have not yet yielded any progeny, a condition which is generally required in order to ascertain that a purely tetraploid strain of a species has been produced.

The senior author has had experiments in progress since the spring of 1938 for the purpose of inducing polyploidy in different shrubs and trees of horticultural or forestry value. In this connection the following list is given of those Coniferales species, which have responded positively to colchicine treatments given partly as injections into the vascular tissue of the stem, partly as seed treatments. The two types of treatment are designated I (injections) and S (seed treatment) respectively.

1. Taxaceæ.

Taxus baccata hibernica (I).

2. Taxodiaceæ.

Sequoia gigantea (S), *Taxodium distichum* (S).

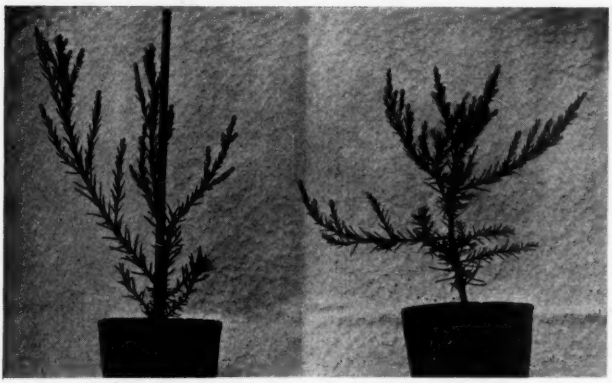
3. Abietaceæ.

Larix europæa (S), *eurolepis* (= *europæa* × *leptolepis*) (I), *occidentalis* (S), *sibirica* (S), *Pinus cembra* (I), *ponderosa* (S), *Abies concolor* (I).

4. Cupressaceæ.

Thujopsis dolabrata (I), *Thuja gigantea* (S), *occidentalis* (S), *Chamæcyparis Lawsoniana* (three different proveniences of *glauca* type, S), *Juniperus chinensis Pfitzeriana* (tetraploid; SAX and SAX, 1933, I), *communis suecica* (I), *squamata Meyeri* (tetraploid; JENSEN and LEVAN, unpublished, I).

For the present only the treatments of *Sequoia* will be dealt with in some detail. In the spring of 1939 seeds of *Sequoia gigantea* were put to germination on filter paper moistened with 0,2 % colchicine solution in Petri dishes. Most of the germinating seeds exhibited very typically



a b

Fig. 1. The appearance of the *Sequoia* plants $1^1/_2$ years after the treatment, *a*: treated plant, *b*: control plant.

the colchicine effects: swollen tissues, inhibited or slow longitudinal growth, etc. They were planted in seed boxes. Many of the treated plants and the controls were damaged during the summer by some fungus disease, so that in the spring of 1940 only 3 among the treated plants remained, which were transplanted into fixing pots. In their further development two of them exhibited a constantly deviating appearance suggesting polyploidy. Their colour was dark green, their branches were coarser and more erect, their needles broader and thicker than normally (Fig. 1). Also their roots were markedly thicker than the roots of the control plants. In the summer of 1940 new colchicine treatments of *Sequoia* seeds were performed, this time with 0,1 % solution. 20 specimens or 50 % of the surviving treated material showed remaining evidence of polyploidy.

One of the plants from the first treatments was fixed in June, 1940, together with several control plants. The fixations were made in NAVASHIN and LA COUR 2BD. Both fixatives gave good result, but the exact chromosome number is difficult to determine. It could be decided with certainty, however, that normal *Sequoia gigantea* has $2n = 22$, while the treated plant investigated exhibited $2n = 44$ in the whole root system, tested on three different occasions.

The root chromosomes of *Sequoia gigantea* have been studied earlier by GOODSPEED and CRANE (1920), who stress the difficulties in getting

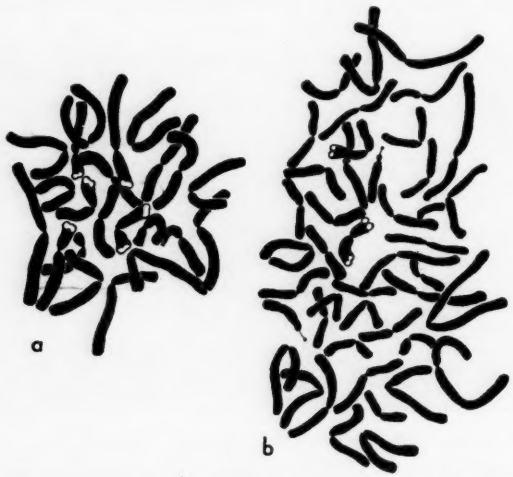


Fig. 2. Somatic chromosomes of *Sequoia gigantea*, *a*: control plant, *b*: treated plant. — × 2500.

exact counts in this material: »We have uniformly counted from 21 to 24 chromosomes, but never a greater number» (l. c. p. 349). As to *Sequoia sempervirens* LAWSON (1904) writes: »As near as could be estimated, there are 16 chromosomes in the gametophyte and 32 in the sporophyte» (l. c. p. 24). GOODSPEED and CRANE (l. c.) do not agree in this number for *Sequoia sempervirens:* »In sections of root-tips of *S. sempervirens* we have made counts which only in rare instances confirm LAWSON's report. The difficulties are great in such material, however». They draw the conclusion that both species have the same chromosome number, viz. $n = 12$ and $2n = 24$. In a later study by DARK (1932) *Sequoia sempervirens* again failed to furnish any exact count. The somatic number was estimated at »near to fifty». Also SAX and SAX (l. c.)

found the chromosome number of *Sequoia sempervirens* to be polyploid: »Although the exact number of chromosomes could not be determined, there were more than 40» (l. c. p. 369). BUCHHOLZ (1939 a, b), working on the embryology of the two *Sequoia* species, determined their chromosome number in mitoses of the gametophytes. The haploid number 11 is given for *Sequoia gigantea* and 22 for *Sequoia sempervirens*, the latter number being reported »provisionally only».

The numbers 22 and 44, given in this paper for normal and tetraploid *Sequoia gigantea,* are probably exact, since they were controlled in several different fixations. It may be pointed out, however, that, as a rule, it is impossible to find more than one or two good metaphase plates in each root tip in spite of a great abundancy of mitoses. This is mainly due to the considerable length of the chromosomes. The largest chromosomes are up to 11 μ and their breadth is nearly 1 μ. They are often crowded rather densely in the plate, and only the region close to the centromeres is orientated on the plate. The long arms are stretched out towards the poles and make the plates difficult to analyse. There are differences in size within the idiogram. The shortest chromosomes are about 4 μ in length. The centromeres are in most chromosomes located medially or submedially, but 2 chromosomes in the diploid and probably 4 chromosomes in the tetraploid are subterminally inserted. In the tetraploid these subterminal chromosomes sometimes show a small satellite, proximally attached (Fig. 2 *b*), but the occurrence of the satellite is by no means regular. As has been shown earlier in several materials, the chromosome size of the tetraploid is on an average somewhat smaller than in the diploid. In the case of *Sequoia*, it seems to be the chromatic quantity which has decreased, while the chromosome length is about the same.

The two *Sequoia* species evidently have different chromosome numbers, *Sequoia gigantea* being a diploid and *Sequoia sempervirens* a tetraploid. Two other spontaneously tetraploid coniferous plants are found within the genus *Juniperus* (see above). The basic number 11 in *Sequoia* is not unique in the family Taxodiaceæ. According to SAX and SAX (l. c.), this number is found also in *Taxodium distichum*, *Cryptomeria japonica* and *Taiwania cryptomerioides*. This number prevails also in Cupressaceæ, while, as is well known, the Abietaceæ family is characterized by the basic number 12.

Helsingborg and Svalöf, September 1940.

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MUTATION EXPERIMENTS IN BARLEY

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DURING the last ten years extensive investigations of induced mutations have been carried out at the Institute of Genetics and the Swedish Seed Association, Svalöf. Theoretical and practical aims have in this way been combined. Thanks to a donation by A.-B. Saltsjöqvarn, Stockholm, it has been possible to extend these investigations to include a number of plant species of practical importance, although principal attention is still being paid to cereals. The vital mutations obtained in barley make it probable that plant species, which have not previously been cultivated with advantage in Sweden, may become important also in this country after a variational increase by the aid of X-radiation. Experiments are at present being made on a large scale with barley, oats, wheat, soya beans, brown beans, flax, hemp, lupin, meadow-grass, etc.

The theoretical investigations have been mainly devoted to determining the dependence of the frequency of mutations and the type of mutation on the X-ray dosages and cell environment at the time of irradiation. Certain results obtained in barley have already been published by the present writer (GUSTAFSSON, 1940). In this brief report only problems of general biological interest will be discussed.

THE PROPORTIONALITY OF DOSAGE AND MUTATION FREQUENCY.

Since the publication of the comprehensive works of TIMOFÉEFF-RESSOVSKY and his co-workers in 1935, 1936 and 1937 it has been regarded as practically axiomatic that mutation frequencies following X-radiation increase in direct proportion to the dosage. This law of proportionality is probably generally applicable to the sperms in *Drosophila*, but it has not yet been proved whether the law applies to other material (particularly plant material). As pointed out by TIMOFÉEFF-RESSOVSKY, divergencies from a direct proportionality may be associated with various kinds of selection phenomena. Unfortunately the linear increase has not been shown even in *Drosophila* to any great

extent in other than sex-linked lethals. In the 1936 work, it is true, visibles also seem to follow the law of proportionality, but their total number is rather small. Moreover, it is conceivable that the combination of the material may involve biological and statistical errors (see below).

Seed samples of the pure line Gullkorn (Golden Barley) were irradiated with 5000 r and 10000 r. The sterility properties of the X_1 generation were estimated, and in laboratory cultures the number and nature of the chlorophyll mutations in the X_2 generation were determined. The cell environment at the time of irradiation was varied in the first place with respect to the degree of hydration. In this way it was possible to carry out an analysis of the mutation frequency and mutation type in relation to sterility, dosage and metabolism. In the last experiment performed 203 mutations were classified.

At 5000 r and 10000 r seed series with 10 % H_2O gave 19 and 22 mutations respectively, while the expected number in direct proportionality is 14,55 and 26,45 (different numbers of X_1 plants in the two series). The P value for this difference amounts to 0,16, i. e. no certainty exists that a direct proportionality is *not* present. Using the same dosages, seed series with 15 % H_2O at the time of irradiation gave 26 and 36 mutations respectively, while the expected numbers are 21,88 and 40,12. The P value is here higher, viz. 0,28. Thus in both cases there is a good agreement with what may be expected in accordance with the *Drosophila* results.

This agreement is only apparent however. As the sterility of each X_1 plant was determined, the proportionality in the different sterility classes can be estimated (Table 1). In all these examinations the sterility classes have been fixed at 0—30 %, 30—70 %, 70—90 % and 90—100 % *fertility*. The reason for this is explained in the previous work mentioned above. It can at once be said that mutations arising at the same time as great decreases in fertility (30—90 % fertility) are either dependent on or have been formed simultaneously with more or less pronounced chromosome disturbances and chromosome rearrangements of various kinds, while the chromosome disturbances are much fewer and smaller in the 90—100 % fertile plants. The, strictly speaking, intragenic mutations arising independently of genome rearrangements should thus be found especially in this group.

Of the 103 mutations recorded in Table 1, 45 arose at a dosage of 5000 r and 58 at a dosage of 10000 r, the expected numbers in direct proportionality being 36,46 and 66,54. The P value is 0,08, i. e. lower

than in the two series of seeds separately. There is, however, no certainty of a deviation from the proportionality being present.

In the 30—70 % class the dosage of 5000 r gives a higher mutation frequency than the dosage of 10000 r. The P value of the difference against a direct proportion is $< 0{,}01$. (The significance of this P figure is diminished, as in some other cases, owing to the small number of mutations.) The expected numbers are 1,04 and 8,96 as compared with the obtained numbers 4 and 6. However this lack of proportionality may be explained — the writer agrees with the selection interpretation — it is obvious that the law of proportionality does not apply to plant progenies with a high X_1 sterility.

In the 70—90 % class, in which the irradiation has brought about an evident, although very slight, increase of sterility, the number of mutations obtained amounts to 16 and 40 as compared with the expected number 14,71 and 41,29. The P value of this difference is 0,70. The proportionality law still applies to mutations associated with comparatively few chromosome disturbances.

In the 90—100 % class, in which intragenic mutations should accumulate without concomitant chromosome disturbances, 25 and 12 mutations arose at 5000 and 10000 r respectively, as compared with the expected numbers 18,10 and 18,90. The P value of the difference against proportionality amounts to 0,02—0,03, i. e. there is a strong indication that no direct proportionality exists in the material.

This will be still more evident if the

TABLE 1. *The relation of dosage and plant sterility to mutating.*

Series		Fertility of X_1 plants			Σ	Proportion 10000 : 5000 r 30—70 %	Proportion 10000 : 5000 r 70—90 %	Proportion 10000 : 5000 r 90—100 %
		30 — 70	70 — 90	90 — 100 %				
1939: I: 17, 20 5000 r	Σ plants Σ mutat.	13 4 = 30,8 %	213 16 = 7,5 %	381 25 = 6,6 %	607 45 = 7,4 %	0,77 : 2,23 (Exp. 2 : 1)	1,92 : 1,08 (Exp. 2 : 1)	1,44 : 1,56 (Exp. 2 : 1)
1939: I: 21, 24 10000 r	Σ plants Σ mutat.	56 6 = 10,7 %	299 40 = 13,4 %	199 12 = 6,0 %	554 58 = 10,5 %			

four values for this class at different water content and dosages are compared with each other. These four values are 6,4 %, 6,7 %, 6,3 % and 5,9 % mutations (GUSTAFSSON, 1940, p. 19, Table 8.). In X-radiation of dormant seeds the number of mutations, which are strictly speaking intragenic, appears to show a threshold value of about 6 %, above which the mutation frequency cannot go without an increase in the plant sterility.

To sum up, it may thus be said that the direct proportionality in barley is a pseudophenomenon. It does not apply to mutations associated with intensive chromosome disturbances nor to intragenic mutations arising without chromosome disturbances or without an increase in sterility. Generally speaking, however, it still holds good of mutations arising simultaneously with small, though evident, fertility changes. An interesting point is that this group of mutations corresponds most closely to the lethals in *Drosophila*, which are to a great extent cytological and genic deficiencies.

In the 1940 paper mentioned above it was shown that *xantha* mutations give a much higher increase in frequency when the dosage is doubled than the *albina* mutations. The rate of the *albina* mutations is 1,10 : 1, while that of the *xantha* mutations is 7,67 : 1. The difference between the two groups of mutations is probably statistically significant ($P = 0{,}05—0{,}04$). Thus there exist differences in proportionality not only in regard to the sterility ranges but also in regard to the mutation types. The above-mentioned circumstances is all the more noteworthy as the *albina* mutations are subject to selection to a lower degree than the *xantha* (and *viridis*) mutations.

The best agreement with the direct proportionality is shown by the *viridis* mutations (the seedlings contain carotin, xanthophyll and chlorophyll, but in varying proportions). At 5000 r 7 mutations are equivalent to 12 at 10000 r. The expected values are 6,72 and 12,28. $P = 0{,}90$.

Alboviridis mutations (the seedlings have different colours at the base and tip) give 11 and 13 cases as compared with the expected numbers 8,49 and 15,51. $P = 0{,}29$.

The *xantha* mutations (the seedlings contain only xanthophyll and carotin) arise only once at 5000 r, on the other hand, 7 times at 10000 r. The expected numbers are 2,83 and 5,17. $P = 0{,}18$.

The *albina* mutations, however, behave quite differently. In this case the number of mutations obtained is 24 and 24 as compared with the expected number of 16,99 and 31,01. The P value of this difference

will be 0,04. While the *viridis*, *xantha* and *alboviridis* mutations show a good agreement with the law of proportionality — if summarized their expected numbers are 18,40 and 33,60 against the obtained values of 19 and 33, P = 0,87 — this law probably does not hold good of the *albina* group. According to other results, this type of mutation is in its mode of origin independent of chromosome rearrangements and increase of sterility, in other words, the *albina* mutations arise principally as intragenic changes. Thus, here again it appears that »visibles» associated with chromosome disturbances follow the proportionality law, but that intragenic mutations arise in other proportions. This cannot be due to conditions of selection, since, as mentioned above, *albina* mutations are not so readily subject to selection as *xantha* and *viridis* mutations.

This divergency will be seen still more clearly if the different mutation types are also divided into sterility classes (30—90 % and 90—100 %). None of the sterility classes, except the 90—100 % *albina* class, differs statistically from the rate of proportionality. The P values of the 7 groups are: 0,04—0,03 for the 90—100 % *albina* class, 0,19 for the 30—90 % *albina* class, 0,21 for the 30—90 % *alboviridis* class, 0,46 for the 30—90 % *xantha* class, 0,46 for the 90—100 % *alboviridis* class, 0,69 for the 90—100 % *viridis* class and 0,76 for the 30—90 % *viridis* class. Thus the best agreement is shown by the two *viridis* groups, whereas the poorest agreement is shown by the two *albina* groups, one of which very probably deviates from the proportionality law.

After the above examination it seems to me that the following conclusion is justified: A direct proportionality in barley between dosage and mutation frequency is only apparent. Mutations associated with profound chromosome disturbances (high sterility) do not show direct proportionality, nor do mutations arising in entirely fertile plant progenies. In the latter threshold-values of about 6 % occur after X-radiation of dormant seeds. Mutations which, like lethals in *Drosophila*, are associated with small, but evident, structural changes (70—90 % fertility) show a direct proportionality. Whether this proportionality, too, is only apparent cannot be decided for certain at present. It is nevertheless probable, for even *albina* mutations in the sterile class (30—90 %) show a poorer agreement than other mutation types.

Besides, different mutation types show a different dosage proportionality. *Albina* mutations (especially in the 90—100 % class) do not show direct proportionality, whereas *xantha*, *alboviridis* and *viridis* do so. In other words, mutations that may be considered as

being associated with genome rearrangements show proportionality, while mutations that can be called intragenic do not do so.

From what has been said above, it appears as if the general validity of the proportionality law should be restricted. The complex biological system nucleus—chromosome—gene → mutation probably follows more proportionality schemes than that required by the »Ein-Treffer» hypothesis. But I should like to emphasize once more here that the above results have reference to only two dosage points, 5000 and 10000 r, and that experiments carried out in the spring of 1940 are expected to elucidate the frequency rates in a series of different dosages.

DETERMINED AND DIRECTED MUTABILITY.

In the work mentioned above I considered as probable that definite phenotypic groups of mutations possess homogenous genotypic properties. The following rules generally hold good:

Xantha mutations cannot arise, or do so only with difficulty, in the offspring of completely fertile X_1 plants. Of the 16 mutations obtained in the 1939 irradiated series not one arose in the 90—100 % fertility class, in spite of the fact that this class contains 43 % of all X_1 plants.

Viridis mutations chiefly arise in progenies of highly sterile plants (0—30 % and 30—70 % fertility), in contrast to the *xantha* mutations, which are produced especially in the 70—90 % class. Thus the two groups of chlorophyll mutations are determined by the increase in sterility and thereby by chromosome disturbances, but these are different in the two groups.

Alboviridis mutations occupy on the whole a position between *viridis* and *xantha*. They, too, are correlated with the occurrence of sterility.

In these three cases we can therefore speak of a certain determination of the process of mutation. Every type of mutation, and consequently the individual cases of mutation, do not arise at random, they are associated with definite changes in the genome, differing more or less in the different cases.

In certain respects the process of mutation can also be directed. *Alboxantha* is a type of mutation that has occurred only once spontaneously, and even after irradiation it is rare. It is devoid of chlorophyll but, in addition, the occurrence of carotin and xanthophyll

is localised, so that the tip is entirely white with a sharply defined boundary between the white and the yellow. An incorrect classification is therefore practically impossible. In very careful experiments this type of mutation did not arise at all after the irradiation of seeds with a low water content (10 % H_2O), somewhat more readily in seeds with 15 % H_2O, but fairly easily in seeds soaked in water or treated with auxin about 24 hours before irradiation for the purpose of starting germination. The percentages of mutations are 0,00, 0,17 and 0,99. The numbers of X_1 plants in the three cases are 586, 575 and 604. If these results can be generalised, then the process of mutation must be directed in so far as *alboxantha* is concerned. An interesting point is that its occurrence is not determined by the number of chromosome disturbances *per se*, for the mutation frequency is higher in entirely fertile plants of the wet series than in ± sterile plants of the dry series. Thus hydration itself seems to influence the genes or the chromosomes in a definite manner so that they respond to X-radiation with an increased proportion of *alboxantha* mutations.

While *alboxantha* arose exclusively in wet series, *albina*, *viridis* and *xantha* occupy an intermediate position between *alboxantha* and *alboviridis* or *tigrina*, for the two last-mentioned groups are produced at least to the same extent in both dry and wet series, in fact, there seems to be a certain tendency for *tigrina* to arise more readily in seeds having a low water content. Four *tiger* mutations arose in the 1939 experiments, all of them from X_1 plants of seeds having 10 % or 15 % H_2O, while the water-treated seeds, in spite of the great increase in the total frequency of mutations, did not produce a single example. The difference, however, is not statistically significant. The *alboviridis* mutations show a frequency of 2,05, 2,09 and 1,99 % respectively in the three groups of seeds. They are thus independent of the degree of hydration and probably also of the general metabolism of the cell at the time of irradiation.

Viridis mutations greatly increase in frequency after soaking, although they also occur in dry series, more especially in the offspring of sterile plants. This dependence on hydration, however, is strictly governed by law (GUSTAFSSON, 1940, Table 10). The mutation frequency of germinating seeds and of seeds with 10 % H_2O gave a ratio of 4,09 : 1. The great increase, however, is entirely due to the enhanced propensity of the *sterile* plant progenies to produce *viridis* mutations. The ratio in the 30—90 % class is 9,50 : 1, whereas in the 90—100 % class it is only 1,55 : 1. Hydration brings about regulated changes in

the sensitivity of the chromosomes, by means of which the *viridis* mutations increase in number.

The *xantha* mutations, it is true, increase considerably with an increased hydration (from 0,68 % at 10 % H_2O, via 0,70 % at 15 % H_2O up to 1,32 % following water and auxin treatment), but this increase is only apparent, since *xantha* mutations arise exclusively in the offspring of ± sterile X_1 plants. If the percentages of mutations in the sterile range are compared, the ratio for soaked seeds and seeds with 10 % H_2O will be 1,05 : 1. Thus after intense hydration the frequency of the *xantha* mutations is directly proportional to the number of sterile plants.

An intentional direction of the process of mutation may thus take place to a certain extent in the following ways:

1) *Albina* mutations, which do not give a direct proportionality between mutation frequency and X-ray dosage, arise more readily than other chlorophyll types at low dosages and to a great extent in completely fertile plant progenies, in which *xantha*, *alboviridis* and *viridis* mutations are rare or do not occur at all. In fertile plant progenies of water-soaked series they arise about three times as frequently as all other types together, in the sterile plant progenies somewhat less frequently than the other types. Thus in order to obtain an excess of *albina* mutations completely fertile X_1 plants from the water-soaked series should be selected.

2) *Xantha* mutations are most easily produced at relatively high dosages and are formed only in the offspring of slightly but evidently sterile X_1 plants, where they comprise approximately 16 % of all chlorophyll mutations at 10000 r.

3) *Alboviridis* mutations are produced as easily in dry series as in wet, but chiefly in the progeny of sterile plants, where in the dry series they comprise about 40 % of all mutations.

4) *Alboxantha* mutations are formed only after an extensive hydration, when germination processes have set in. They do not seem to arise in dry seeds (10 % H_2O).

5) *Viridis* mutations are most easily produced in material with greatly increased sterility and then mainly in the offspring of highly sterile plants. The increase in sterility can be brought about by increasing the dosage. Soaking in water produces changes in the chromosome sensitivity, which in turn increases their number. In contrast to *albina* they are not often formed in fertile progenies and,

unlike *xantha*, are chiefly produced in highly sterile offspring, where translocations, deficiencies and position effects are accumulated.

6) Finally, *tigrina* mutations possibly arise exclusively by X-radiation of dry seeds.

These inferences should not of course be taken to imply that the different type of mutations are formed invariably and in different materials in accordance with the rules mentioned. As only one pure line of barley has been investigated so far, the results in their present form may be valid only for that line. Under all circumstances they nevertheless seem to indicate that a certain environmental adaptation of the mutation process is possible. How this is to be interpreted from a chemicophysical point of view is of course at present wrapt in obscurity. Possibly the X-rays act in a specific way only in a certain definite condition of the nucleus, the chromosomes, the reproductive system. If the cell environment is changed, the direction of mutation is changed too.

The classification of vital mutations with respect to cell environment and dosage has only been possible to a very small degree. So far their number is too small to permit a statistical treatment. Of ten so-called *erectoides* and *erectum* mutations, which have arisen in controlled series, not one has been formed in the progeny of 90—100 % fertile plants. Perhaps the *erectoides* mutations follow the same rules as the *xantha* types.

VITAL MUTATIONS.

In addition to a great many chlorophyll mutations of different kinds, a number of morphological and vital forms have also arisen in recent years. The majority of these latter forms fall within the known variation sphere of cultivated barley. In spite of their being non-lethal, some of these mutations can hardly be called vital, for instance, dwarfs or those morphological variants which, owing to the complete sterility of the homozygote, like the majority of chlorophyll mutations, have to be kept alive year after year through the heterozygote. Many mutations, however, are completely vital and in solitary characters, such as straw-stiffness, size of kernel, earliness, constitute practical improvements as compared with the original line. It has not yet been established whether any of these mutations show a higher yield capacity than the mother strain. It may be mentioned here, however, that NILSSON-EHLE, who several years ago obtained mutations of an *erect-*

oides character (see below), was able to prove that in intensive nitrogenous fertilisation one of them was equal to the original line as regards yield.

In the group of vital mutations, to which the solitary *viridis* or *alboviridis* mutations — which produce seeds even in a homozygous condition — should not be referred, it is possible to distinguish two sub-groups: 1) *Morphological mutations* in which, in addition to changes in physiological properties, also morphological characters are altered. As a rule they segregate sharply in intercrossings or in crossings with the original line. 2) *Physiological mutations* which when cultivated alongside the original can, it is true, be clearly distinguished from the latter, but only in properties relating to straw-height, straw-stiffness, lateness, earliness, tillering capacity, etc. No exhaustive analyses of the crosses have yet been made, but it is probable that the segregation is unsharp.

There is hardly any well-defined boundary between the two sub-groups, because all mutations observed were pleiotropic. Besides, the winter barley-like variants, which segregate sharply and are easily distinguishable from both heterozygotes and normal homozygotes by their extreme lateness, form a transition between the two sub-groups. But these variants must be called physiological rather than morphological mutations.

The commonest group of vital mutations consists of the so-called *erectoid* mutations, which are easily distinguished from the original line (Gullkorn), a typical *nutans* line, by the compact ears. Morphologically they resemble the *erectum* barleys (e. g. Primus) already in cultivation, although the majority differ in the nature of the base of the seed. In its typical form *erectum* barley has a transverse nick at the seed-base (TEDIN and TEDIN, 1927), by means of which it can be easily distinguished from all *nutans* types. The ear of the *erectoides* mutation, besides being more compact, is also erect, and the straw is often shorter and stiffer. When crossed with each other the *erectoid* types produce the *nutans* barley in F_1 and in F_2 segregate *nutans*, *erectoid* and *zeocriton*-like types, as already shown by NILSSON-EHLE (1939) either in the ratio $9 : 6 (= 3 + 3) : 1$, if free combination is present, or in divergent ratios with a deficiency of the double recessive (*zeocriton*) in the event of linkage. In crossing with the original line, the *erectoides* give a normal (or intermediary) F_1 and a segregation of $3 : 1$ (or $1 : 2 : 1$) in F_2. The number of *erectoid* in contrast to chlorophyll mutations seems to be limited. In a cross between one of the

author's mutations and one of NILSSON-EHLE's the F_1 was *erectoid* and the F_2 showed no segregation, a result obtained already by NILSSON-EHLE after crossing two of his own *erectoid* mutations.

In 1940 four *erectoid* mutations were included in comparative yield trials, three or four in propagation while four new cases were observed. Altogether the writer has found 11 (12) cases of mutations. In addition to these *erectoides* mutations, which have the compact ears and the kernel size of the *erectum* type but have no transverse nick at the base of the kernel, an extreme *erectum* mutation (*erectoides* 3) has been obtained, which also possesses the last-mentioned character. (The mutation in question was found by Mr. C. G. VON SYDOW, practical assistant at the Institute of Genetics.) This mutation arose in the 1937 experiments as a semidominant mutation in the X_1. The X_1 plant was up to 97 % sterile. Only one seed was set, which gave rise to the original, completely fertile X_2 plant. The X_1 plant differed in the type of the ear distinctly from the original line, and when crossed later with the latter the mutation was found to be (semi-)dominant. The F_1 individuals also resemble the mutation in such characters as breadth of leaf and thickness of straw. The F_2 has not yet been analysed. As regards length of ear and straw-height the F_1 shows heterosis. The marked sterility of the X_1 plant, as in the entire X_1 generation (from 510 irradiated kernels only 20 plants arose, the average fertility of which was 32,4 %), points to far-reaching chromosome rearrangements, at the same time as the occurrence of one or more gene changes. Therefore an entirely new state of equilibrium has taken place in the genome.

Six *erectoid* mutations have been analysed with respect to the number of barbs on the lateral nerves of the seeds. Gullkorn possesses 4,45 barbs per nerve while the *erectoid* mutation that arose from the most fertile X_1 plant (with >70 % fertility) has 4,30 barbs per nerve, i. e. about the same as the original line. Two *erectoid* mutations, originating from X_1 plants with a fertility of 30—70 %, have respectively 1,50 and 2,95 barbs per nerve, and the extreme *erectum* mutation (the X_1 plant had 3 % fertility) has 0,00 barbs per nerve. Two mutations from X_1 plants of unknown fertility were found to have 3,15 and 0,75 barbs per nerve. Although no conclusions can yet be drawn, these figures indicate that the more marked the sterility, and consequently the chromosome disturbances, the more extensive will be the morphological deviation of the mutations. This does not of course imply that the position effect plays a dominant rôle — on the contrary that can be

disproved — but that the number of mutating genes increase to the same extent as the number of chromosome rearrangements.

Fig. 1 illustrates the ears of five *erectoid* mutations, the original line on the extreme left. In Fig. 2 will be seen kernels from seven different mutations, Gullkorn on the extreme left in the upper row. The extreme mutation (second from the left in the lower row) has the

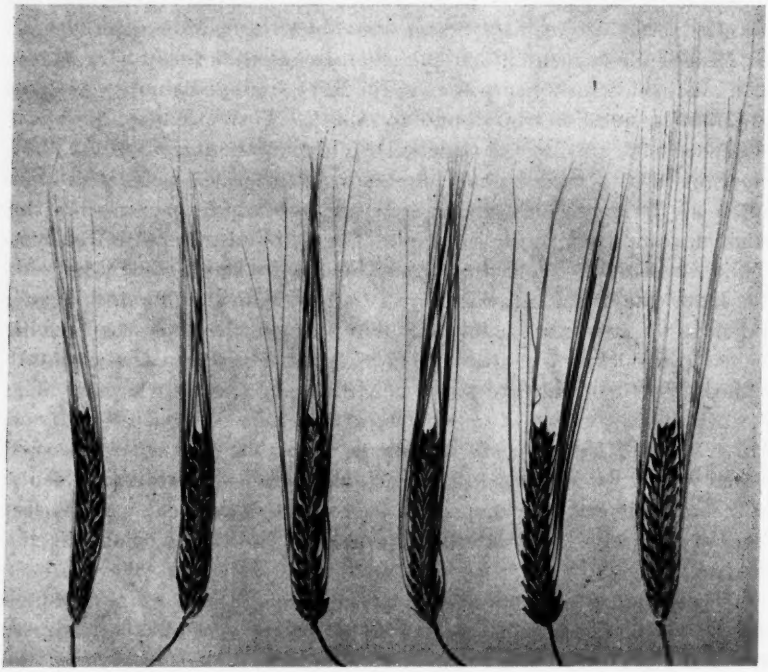

Fig. 1. Five induced *erectoides* mutations in barley. From left to right: Gullkorn (Golden barley, the mother-line), *erectoides* 4, *erectoides* 2, *erectoides* 7, *erectoides* 1 and *erectoides* 3 (= the extreme *erectum*). — Photo H. OLSSON, Svalöf.

largest seeds. Many *erectoid* mutations have fairly compact and broad kernels, which is reflected in their spread position in the ear.

A specially interesting morphological mutation was described by GUSTAFSSON and ÅBERG in 1940. *The glumes were lemma-like* and furnished with long awns. The same type of mutation, but differing in the length of the awns, arose in the summer of 1940. It has not yet been ascertained, however, whether this new mutation is due to the same genotypic change as the preceding one. The two mutations were

produced in the offspring of X_1 plants with a fertility of 16 % and 59 % respectively. The mutation obtained first was included in the 1940 yield trials and is completely fertile (X_2—X_4). In crossing with the original line it is recessive. The second mutation arose in the same X_1 series as the extreme *erectum* type (the X_1 plants showed an average fertility of 32,4 %).

Two *winter barley*-like mutations were obtained in the 1939 experiments, one from an X_1 plant with 30 % fertility, the other from

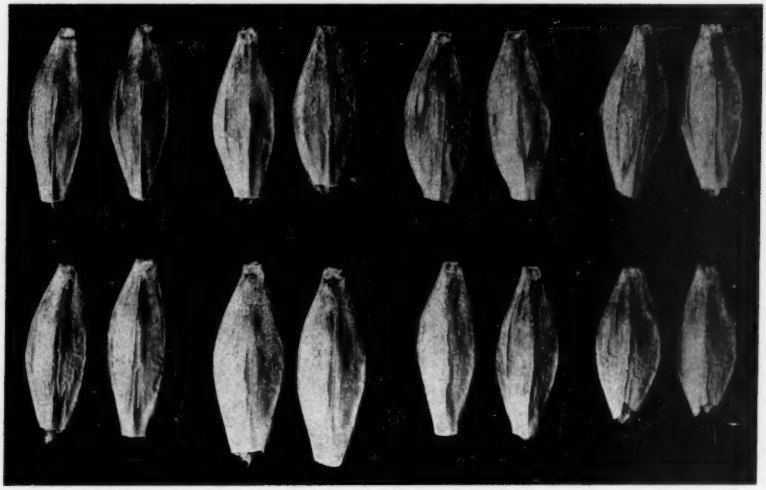

Fig. 2. Kernels of seven *erectoides* mutations. From left to right, upper row: Golden barley, *erectoides* 4, *erectoides* 2, *erectoides* 7, lower row: *erectoides* 1, *erectoides* 3 (= the extreme *erectum*), *erectoides* 5 and *erectoides* 6. — Photo H. Olsson, Svalöf.

an X_1 plant with 43 % fertility. The winter barley character is not so pronounced that the mutations cannot wholly or partly produce ears or seeds. The ears are not formed, however, until the end of the vegetative period, long after the normal plants have passed the flowering stage. Moreover, one of the two types is so late that it hardly has time to mature. The other type, on the contrary, is quite fertile. Even in these two mutations a number of properties changed simultaneously. According to the preliminary examination made in 1939, the mutation originating from the X_1 plant with 43 % fertility was almost entirely without barbs on the seed nerves, while the other mutation had pointed lateral florets in the ears. The latter was also very tall and broad-

leafed (»reed-like»). No crosses have yet been made between the two types and with Gullkorn.

In the 1940 experiments three X_2 and X_3 cases of *six-row* mutations arose in an otherwise normal material, one heterozygote and two homozygotes. The mother plants were 25 %, 90 % and 49 % fertile respectively. They were all formed, singularly enough, in the dry seed series. As solitary plots of six-row barley were cultivated adjacent to the two-row barley during the years 1937—1939, there is a slight possibility that a mechanical interference took place. All three mutations cannot, however, be explained in that way. Their progenies will at once clear up the matter.

Mutations of great fundamental interest are those involving changes in *kernel size* and *kernel colour*. None of them has yet been tested in comparative trials. While Gullkorn, before maturing, has yellowish green kernels with strands of anthocyanin along the nerves, one of the kernel colour mutations has brownish kernels, which are about one-third larger than those of the original line. Besides, the stem and awns have a high content of anthocyanin (brownish red—brown). The fertility of the original plant was 89 %. Another mutation had light yellow kernels instead of yellowish brown, and also lacked the rich streakiness of Gullkorn. But in these mutations, too, the straw and the awns were deeply anthocyanin-coloured. The fertility of the mother plant was 100 %. Three more kernel colour and kernel size variants (the fertility of the mother plants was 73 %, 82 % and 95 % respectively) was observed in the X_2 material in 1940. At the same time such properties as straw-stiffness and earliness were also changed. The occurrence of these mutations proves that the size of the kernels can be easily changed without any alteration in the type of ear (cf. the *erectoid* types) provided a sufficiently large material is available.

These mutations form a special group among the physiological mutations, which have been obtained on a large scale. The first physiological mutation was observed in the summer of 1937; it sets ears and matures 3—4 days *later* than Gullkorn. It also differs from Gullkorn in having taller straw and longer, somewhat sparser ears. The stiffness of the straw and the type of ear are normal. This mutation was included in the 1940 comparative yield trials. Its fertility and vitality are not lowered. Since then *straw-height* mutations have been obtained frequently. Completely fertile mutations with lower straw-height (the height of the straw was about the same as that in the

improved Danish strains Kenia and Opal) have also arisen. The lower straw-height is often accompanied by increased *straw-stiffness*. One or two of these mutations will be included in comparative yield trials in the summer of 1941. Two straw-stiffness mutations are included in the 1940 yield trials.

Variations respecting *time of maturing* are very pronounced in a number of mutations. A change in the direction of a prolonged vegetative period seems to occur most easily. In 1940 the *erectoid* mutations matured at the same time as or a little earlier than Gullkorn (in 1940 the extreme *erectoid* mutation was a week or ten days later), and in the 1940 yield trials one of the physiological mutations (a straw-stiffness mutation) ripened one day or two before Gullkorn. A leaf-colour mutation, also included in the 1940 yield trials, matured in 1939 about 5—7 days earlier than a neighbouring plot of Gullkorn, but in comparative cultivation in 1940 it was 5 days later. It cannot yet be said whether this delay was due to the abnormal weather conditions prevalent this summer. No intentional selection for increased earliness has been made in barley, but has been done in X_2 material of soya beans. It has been established, however, that maturing differences in the direction of increased earliness as well as increased lateness can be induced, although increased lateness occurs more readily.

In addition to these three types of vital physiological mutations (straw-height, straw-stiffness, time of maturing) *chlorophyll-content* mutations have also been obtained (no exact estimations have yet been made). During the first part of the vegetative period one of these mutations — the earliness mutation already discussed — is almost normal, but after earing it rapidly turns yellowish and at maturity is deeply yellowish green. It should perhaps be characterized as a vital, entirely fertile chlorophyll mutation of a *lutescens* type. Another leaf-colour mutation has, in transmitted light, markedly clearer leaves, without being for all that a chlorophyll mutation. This mutation, too, is completely fertile. Mutations with a darker leaf-colour or thicker waxy coating have not been searched for and are almost impossible to detect without physiological aid unless morphological changes appear at the same time. *Erectoid* and straw-length mutations with an increased waxy coating occur.

These investigations, which have been going on for only two years on a large scale, prove that a pure line can be split up in many directions, so that a new population is produced, built up on the fundamental genotype of one and the same selected line, and con-

sequently — in contradistinction to the local strains — not on several more or less valuable original types. It cannot yet be said whether any biotype in the population produced by induction will prove to be so much superior to Gullkorn that it can be used directly for practical purposes. In the spring of 1940 the high-yielding strain of barley Maja (originating from the cross Gullkorn × Binder) was X-rayed for the purpose of turning it in a similar manner into different morphological and physico-chemical directions. So much can be gathered from the results already obtained that by the induction method vital mutations can be produced, which in individual characters constitute a practical improvement of the original line at the same time as their fertility and vitality are adequate. Moreover, in some instances mutations have been obtained which enrich the variability of cultivated barley.

What then is the highest mutation frequency that can be obtained and what are the most suitable conditions for an experimental production of viable variants on a large scale? The series that has been most thoroughly studied is mentioned in the author's paper of 1940 (Table 2), viz. 1937: 110. After desiccation above H_2SO_4 and X-radiation only 30 X_1 plants, having an average fertility of 29,7 %, resulted from 505 seeds. Six chlorophyll mutations arose in the X_2 progeny. These 30 X_1 plants produced 110 ears, which gave rise to 110 rows of X_2 plants. In the X_3 laboratory analysis of these 110 rows of X_2 plants the following mutations were obtained: 4 *albina*, 2 *xantha* and 3—4 *viridis*. Thus the total frequency of chlorophyll mutations was 30—33 %. Besides, dwarf mutations segregated in two X_3 families, and in a third family evidently aberrant seedlings with coarse leaves (= the dwarf mutation mentioned below). In the spring of 1939 106 pedigrees from 28 of the original X_1 plants and 45 of the 110 rows of X_2 plants were planted for field experiments. In this X_3 generation the following mutations were observed: 1 fully fertile, intensely shrubby dwarf, 2 winter barley-like types, 1 leaf-colour mutation (in 1939 regarded as an earliness mutation; see p. 239), 2 straw-stiffness mutations, 2 straw-height mutations and 1 mutation (homozygous in the X_3), highly susceptible to fungi. Of these mutations, the leaf-colour mutation and one of the straw-stiffness mutations were included in the 1940 yield trials, and the majority of the remainder were propagated and their properties, constancy and fertility were controlled.

Altogether at least 9 controlled morphological and physiological mutations, corresponding to a frequency of 32,1 %, arose in these field

experiments. Thus the total mutation frequency for the entire series is 30 — 33 % + 7 % + 32 % = 70 %. This result does not include sterility and qualitatively chemical mutations, nor the more or less probable cases of physiological mutations, which segregated in the X_3 and were not further examined in the X_4. A complete record, supplemented with a chemical examination, would undoubtedly have given a total mutation frequency of 100 % or more, i. e. every X_1 plant would have produced one or more mutations. In spite of the high, partial sterility in X_1 and X_2 nearly all non-lethal mutations are at present fully fertile and vital. In root-mitoses germinating X_1 seeds of this series showed a disturbance frequency of *at least* 71 %. Thus the genome has been entirely split up and profound chromosome rearrangements have taken place. This is reflected in the high X_1 sterility. In X_2, X_3 and X_4 this structural heterozygoty is broken up into a large number of structural homozygotes, among which only the vital combinations survive. Some of the structural homozygotes are associated with morphological and physiological changes. Of the 20 mutations 6 were entirely fertile, vital and apparently constant (one straw-height mutation has not yet been completely examined). Thus the frequency of vital, practically interesting variants from the 30 X_1 plants amounts to approximately 20 %.

Similar experiences have been obtained from investigations of other highly sterile X_1 series. For grain crops like barley a low power of germination in the irradiated seeds and a high X_1 sterility are on the whole favourable for the occurrence of vital and fertile mutations. To be of practical value a gene mutation requires a suitable genotype and an adjusted gene environment. The occurrence of a number of chromosome rearrangements (inversions and translocations) at the same time as the genic change enhances the possibility for the mutated gene to be fitted into a congruous gene environment.

The few induced morphological and physiological mutations obtained in hexaploid wheat (speltoid and straw-height mutations) have arisen from highly sterile X_1 series. Some straw-height mutations are vital and fertile.

To sum up it may be said: The pure line can be split up into different directions. If gene changes and chromosome rearrangements are congruous, they produce vital, fully fertile variants, sometimes enriching the known variation of the species. In certain cases the mutations are equal to the original line in vitality and yielding capacity and occasionally constitute an improvement in individual characters.

New populations should be built up on the genotypic foundation of the highest yielding and practically most valuable varieties.

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SYNCYTE FORMATION IN THE POLLEN MOTHER-CELLS OF HAPLOID PHLEUM PRATENSE

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ONE of the first species in which heteroploid twins were found is *Phleum pratense.* Thus, MÜNTZING (1937, 1938) obtained, among 446 twin plants examined, 9 plants with a deviating chromosome number, 3 »haploids» (2n = 21) and 6 »triploids» (2n = 63). In order to produce a richer material of triploid timothy, which may be of practical importance, a rather great quantity of seeds were germinated last winter at the Cyto-genetic Laboratory, Svalöf. More than $^1/_2$ million germinating seeds were examined, belonging to 5 different mother strains, selected by Dr. FREDRIK NILSSON. On an average 4—10 pairs of twins appeared in every 10000 germinated seeds (see Table 1). In all 384 pairs were secured, and among them 260 pairs and 62 single plants survived until fixing. The majority of these plants had the normal somatic number, 2n = 42, but 11 plants deviated in chromosome number. One of these had 56 chromosomes, 3 plants had 63 chromosomes, and no less than 7 plants were haploid with 21 chromosomes. Compared with MÜNTZING's results, conditions were now the reverse, twice as many haploids as triploids being found in our experiments. The frequency of aberrants, however, is similar in both series (about 2 %).

Although the practical result was rather meagre, as far as the production of triploids is concerned, the haploids obtained must be considered to be of a very great theoretical interest. They will be handed over to Miss H. NORDENSKIÖLD, who will study their morphology and normal chromosome behaviour. The present paper deals with the phenomenon of syncyte formation, frequently occurring during the male sporogenesis especially in one of the two haploid plants, the meiosis of which could be studied this summer. As far as necessary for the understanding of the mechanism leading to the origin of the cell fusions, the normal course of meiosis will also be touched upon.

My thanks are due to Miss MAGNA PALM, Svalöf, for excellent technical help.

I. CYTOLOGICAL OBSERVATIONS.

Fixations of spikelets were made in NAVASHIN after prefixation in CARNOY. Most fixations succeeded well, and the meiotic conditions

TABLE 1. *The origin of twins in Phleum pratense.*

No.	Strain	Number of germinated seeds	Number of twin pairs	% twin pairs	Number of fixed		Number of plants with a deviating chromosome number		
					pairs	single plants	21	56	63
1	0812	103914	41	0,0395	17	5	2	—	—
2	0814	101480	86	0,0847	69	16	2	—	1
3	0817	116209	48	0,0413	35	4	2	—	—
4	0842 (Bore II)	111139	104	0,0936	60	23	—	1	1
5	0804 (Bottnia)	100935	105	0,1040	79	14	1	—	1
Total		533677	384	0,0719	260	62	7	1	3

a b c d

Fig. 1. *Phleum pratense*, the general appearance of two twin pairs, *a* and *c*: diploids ($2n = 42$), *b* and *d*: haploids ($2n = 21$). The haploids are more slender and have narrower leaves and thinner ears than their diploid sister plants. The morphology of the two sister plants of each pair is strikingly similar. — Photo H. OLSSON, Svalöf.

were clearer than is usually the case in haploids. All slides were stained in gentian-violet.

The somatic chromosomes are two-armed with medially to submedially located centromeres. Some chromosomes are clearly asym-

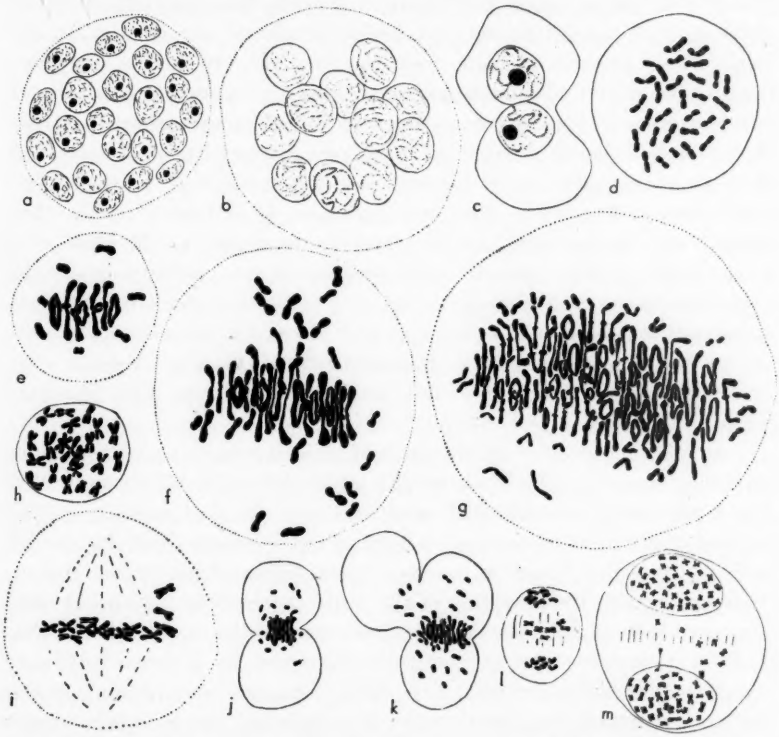

Fig. 2. Meiosis of the haploid *Phleum pratense*, *a—c*: cell fusions during prophase, *d*: a second metaphase plate with 29 chromosomes, *e—g*: first metaphase, *e*: a normal haploid cell with 7 bivalents and 7 univalents, *f*: a syncyte with 3 times the normal number, *g*: a syncyte with at least 150 bivalents and the same number of univalents, *h*: a monad interkinesis nucleus containing 21 chromosomes, *i*: metaphase I with 21 univalents with polarized centromeres, *j—k*: metaphase I in syncytes of *j*: 2 cells, *k*: 3 cells, *l*: normal anaphase I, *m*: telophase I of a large syncyte. — *a—c* × 1200, *d—i* × 2400, *j—m* × 900.

metric. In root cells the chromosome length varies from 3 to 5 μ and at second metaphase, where the contraction is more pronounced (Fig. 2 *d*), from 1 to 3 μ. Chromosome breadth is less than $^1/_2\,\mu$.

Meiosis is very irregular, even if the formation of syncytes is not

taken into consideration. The most striking irregularity is the frequent disturbances in the rhythm of development of the pollen mother-cells. All the different stages of meiosis occur mixed in the same pollen sac, from early pachytene nuclei to pollen tetrads.

At pachytene paired and unpaired threads are seen. The pictures are not clear enough to decide whether trivalents are present at this stage. Most pictures indicate, however, that already at this stage two threads are paired and one unpaired, within each homologous group of chromosomes. At any rate no trivalents occur at metaphase I. Only in one or two doubtful cases did I see any signs of higher associations than bivalents. The typical metaphase I pairing is 7 bivalents and 7 univalents (Fig. 2 *e*). This was found in 14 out of 17 cells. The other 3 cells contained 6 bivalents and 9 univalents or 5 bivalents and 11 univalents. The bivalents are arranged in an ordinary equatorial plate, while the univalents are scattered without order over the cell. At anaphase I the bivalents separate and proceed to the poles, while the univalents form a secondary equatorial plate (Fig. 2 *l*). Usually they are not divided and often fail to be included in the telophase nuclei.

In addition to this typical course of meiosis numerous modifications of it may be seen. One such modification consists in all chromosomes being present at metaphase I as univalents. In that case the pollen mother-cells are often somewhat larger than normally (Fig. 2 *i*), which indicates that this deviation involves a retardation of the normal course. This agrees with the condition of the centromeres, which turn out to be polarized immediately after the disappearance of the nuclear membrane. The 21 univalents are consequently arranged in a frequently very regular equatorial plate (Fig. 2 *i*). The univalents may be divided and form dyad nuclei, but usually they are included into one interkinesis nucleus (Fig. 2 *h*) according to the *Allium amplectens* scheme (LEVAN, 1940). In either case all kinds of irregularities may occur.

Already a superficial examination of the slides reveals the occurrence of an extraordinary difference in size between pollen mother-cells at different stages of meiosis. Intermingled with normal haploid cells, real giant cells with multiplied chromosome sets are present. In extreme cases these large cells fill up the whole pollen sac.

These giant cells are rather common in one plant B 34, while the other plant studied B 33 only shows solitary giant cells. Miss NORDENSKIÖLD kindly informs me that a haploid studied by her is characterized by the same property. The large cells tend to occur more frequently

in certain locules of a flower, while the rest of the locules contain exclusively normal cells.

The origin of these giant cells is not difficult to trace. Already at early preleptotene stages it can often be seen that neighbouring cells fuse. Sometimes cell walls are evidently not formed, and 20 or 30 nuclei may be found lying entirely free in one rounded plasmodium (Fig. 2 *a*).

At pachytene the cell walls begin to thicken. It is now easier to see how the cell walls disappear between adjacent cells. Thus, several cells may coalesce and form large plasmodia, inside which no cell walls are present. The nuclei are first scattered in the plasm, but they are later on gathered towards the middle of the syncyte (Fig. 2 *b*). The different nuclei, however, maintain their individuality, no nuclear fusions being observed before metaphase I. The number of nuclei in each plasmodium varies from 2 up to 20 or 30, syncytes with 4—8 nuclei being most common. Already at pachytene syncytes with a high number of nuclei seem to be retarded in their development and begin to show signs of degeneration.

It is beyond doubt that the fusions may start at different stages in the development of the pollen mother-cells, they may start before leptotene, and they may begin at any stage during the entire prophase. Fig. 2 *c* pictures two pachytene cells with well-developed cell walls, in which the separating wall has been dissolved so that the cells have fused. Such more »recent» fusions have another appearance than the old syncytes. While the latter have acquired a wholly spherical contour, the more recent fusions may be recognized by their irregular outlines, obtained from the cells participating in the syncyte. These more recent fusions form a transition to the phenomenon of cytomixis. The typical picture of cytomixis, viz. a hour-glass-shaped nucleus pressed through a small pore in the cell wall, is met with only in exceptional cases in my material.

The disappearance of the nuclear membrane at the transition to metaphase I reveals a very interesting condition, which is characteristic of the *Phleum* syncytes: no more than one spindle is ever formed, irrespective of the number of nuclei present in the syncyte. This spindle is normal and bipolar, and all the bivalents are orientated on it, while the univalents are left free. In fact, each syncyte behaves at metaphase I strictly as a multiplicate normal metaphase I with its 7 bivalents and 7 univalents. In Fig. 2 *f* 3 nuclei participate in the fusion, consequently 3 times 7 bivalents and 7 univalents may be counted.

In Fig. 2 *g*, where only a small number of the chromosomes present are sketched, more than 20 nuclei have delivered their chromosome material. This syncyte contains at least 150 bivalents and the same number of univalents. It represents the maximum of chromosome content so far found in these syncytes at metaphase I, and seems to be rather unique in my slides. But cells with 50—80 bivalents are found not so seldom. The monstrous cell of Fig. 2 *g* has a perfectly normal spindle. It is sectioned somewhat obliquely and the bivalents are seen in side-view from the upper surface all through the section down to its lower surface. It is of interest to note that each chromosome in this large syncyte is of a decidedly smaller size than normally and shows a decreased stainability, although the fixing is first-rate. Probably the nutrition is made difficult within such a giant plasmodium owing to the remoteness of the centre from the cell walls.

The regular bipolarity of the spindle is valid also in newly formed syncytes. Fig. 2 *j*—*k* show two such syncytes, one composed of 2 cells, the other of 3 cells. The outlines of the cells, as well as the point of fusion, are readily recognized in the pictures. The plate of bivalents is formed somewhere in the centre of the syncyte, while the univalents evidently still remain in their original cell lobes.

The syncytes behave like enlarged normal cells also at anaphase I. The bivalents separate to the poles and the univalents gather at the equator. The regularity of this process is, however, not great and many univalents are left in the plasm, when the telophase nuclei are formed. Fig. 2 *l* and *m* represent a comparison between a normal cell and a syncyte at the end of the first division.

The second division, even in »normal» haploid cells, is subject to such great disturbances that the analysis of it is made rather difficult. At the second metaphase the chromosomes have a somatic appearance, and their number can readily be determined (Fig. 2 *d*). In a number of such plates the following chromosome counts were made:

Number of chromosomes	1	3	4	8	9	10	11	12	13	14	15	16	17	19
Number of cases.....	2	1	1	2	1	2	2	1	3	1	1	1	2	1

Number of chromosomes	20	21	22	24	25	30	37	38	39	Total
Number of cases.....	1	3	1	1	2	1	1	1	1	33

In the formation of cells with numbers exceeding 21 cell fusion may have played a rôle. That the upper limit is as low as 39 shows, how-

ever, that the extreme cases of fusion do not reach the second division. Already interkinesis dyads with high chromosome numbers are much more rare than metaphase I cells, which indicates that the syncytes usually atrophy at the end of the first meiotic division.

II. DISCUSSION.

The formation of syncytes during premeiotic stages and meiotic prophase of *Phleum* shows a certain agreement with the cytomixis phenomenon. Thus, both processes must be regarded as signs of degeneration. Most abnormalities of this kind are found in genetically unbalanced types, as haploids, triploids, hybrids, or among plants modificatively disturbed in one way or other, by heat shocks, by chloralisation, etc. An extreme case of syncyte formation was met with by the present writer in *Petunia* stamens after colchicine treatment of the young growing points. All the tapetum cells and all pollen mother-cells of each locule had fused, forming plasmodia, where in one case as many as 1500 chromosomes were counted (LEVAN, 1939).

According to KIHARA and LILIENFELD (1934), the term cytomixis should be reserved for designating »Übertritte strukturloser Chromatintropfen». Even if this cytomixis *sensu stricto* usually must be regarded as a fixation artefact, it is nevertheless a symptom of deficient wall formation. This is also characteristic of the transport or migration of larger nuclear parts or whole nuclei from one cell to another. This leads to the origin of binucleate pollen mother-cells or syndiploidy, which may be of importance for the origin of polyploidy. Discussions of the literature on cytomixis are found in KATTERMANN (1933), GELIN (1934) and KIHARA and LILIENFELD (l. c.), while a list of the cases of syndiploidy is given by DARLINGTON (1937, p. 65—66). The syncyte formation of *Phleum* may be regarded as an extreme case of syndiploidy, since the cell wall formation is often inhibited within whole pollen sacs. In accordance with the cytomixis the syncyte formation is directly connected with the viability of the plants, the weakest individual showing the most conspicuous syncytes. This agrees with CHURCH's observations in other Gramineae (1929). »The greatest amount of cytomixis is correlated with the greatest amount of irregularities in the maturation divisions» (l. c. p. 75).

The earlier stages of meiotic prophase are considered to be especially favourable for the origin of cytomixis. No doubt, also in *Phleum* the most numerous fusions take place during early prophase, but certain

indications show that it may occur even close to metaphase I. After this stage the conditions of meiosis are so disturbed that nothing can be said about the possible occurrence of fusions at later stages.

The pairing of the chromosomes at metaphase I furnishes some clues as to the limitation of the stage during which the fusions may take place. Thus it should be observed that the number of univalents is always about the same as the number of bivalents present. In other words, the relation univalents : bivalents is the same in normal haploid cells as in the largest syncytes. This shows that the fusions must have taken place after the last division of the archesporium. It also proves that no nuclear fusions occur prior to zygotene. If this were not the case, diploid nuclei would be formed, which would exhibit exclusively bivalents at metaphase I. The study of meristematic tissues in root tips and flower buds also fails to show any somatic cell fusions. Thus, the syncyte formation in *Phleum* is limited to the meiotic prophase.

The normal pairing in haploid *Phleum*, 7 bivalents and 7 univalents, is *per se* of a very great interest, especially when considered in connexion with the findings of MÜNTZING and PRAKKEN (1940) in meiosis of 42- and 63-chromosome *Phleum*. These authors show that only in very exceptional cases are higher complexes than bivalents formed, although the homology and chiasma frequency should permit a frequent formation of multivalents. In the present work proof is brought forward that in two different haploid individuals 7 bivalents are regularly formed. Thus at least two of the three genomes of haploid *Phleum pratense* are homologous and the species may be considered highly autopolyploid. This conclusion is drawn also by MÜNTZING and PRAKKEN (l. c.). The reason why only bivalents are formed in the different chromosomal forms of the species must be due to a specific genotypical predisposition to bivalent formation. How such a mechanism works is still unknown. Crosses between *Phleum pratense* and other *Phleum* species evidently upset this mechanism, for NORDENSKIÖLD (1937) found associations of more than 2 chromosomes in hybrids with *Phleum nodosum* and *alpinum*.

The most remarkable feature of the *Phleum* syncytes is the behaviour of the spindle apparatus at metaphase I. In most earlier cases, where fusions of a great number of cells occurred, the spindle is reported to behave rather irregularly. After the disappearance of the nuclear membrane, as a rule several spindles are found, orientated in different planes within the syncyte. Sometimes each nucleus has a spindle of its own, sometimes different spindles interfere with each other

and fuse. GAINES and AASE (1926) observed in haploid *Triticum compactum* large syncytes, which in their earlier development show a certain resemblance to the syncytes of *Phleum*. Metaphase I is described in the following way: »The chromosomes of each nucleus (of the syncyte) may become oriented on an independent spindle, or the chromosomes of contiguous nuclei may become distributed over a single giant spindle (Text-fig. 8 B). In the latter case a single spindle area is probably developed around two or more of the adjoining nuclei, and as the nuclear membranes disappear in the late prophases there remains no barrier between the chromosomes of the individual nuclei . . . some form of giant »pollen grain» containing small and large nuclei results (Text-fig. 8 C).» (l. c. p. 381). In *Triticum*, however, exclusively univalents occurred, so no direct comparison with *Phleum* can be made. The only case of haploidy, which with respect to the formation of bivalents is fully comparable to *Phleum*, is JØRGENSEN's (1928) haploid *Solanum nigrum*, which regularly formed 12 bivalents and 12 univalents at meiosis. No cell fusions were mentioned in this case.

Thus, the syncytes of *Phleum*, now described, represent a new type, characterized by the fact that the entire plasmodium, originated by cell fusions, behaves as one individual entity, i. e. it acquires strict bipolarity. Evidently the extranuclear or centrosomic part of the spindles belonging to the different nuclei of the syncyte have the ability of fusing and after that of acting as one organ of the syncyte.

SUMMARY.

In two plants of haploid *Phleum pratense* ($2n = 3x = 21$) cell fusions are frequently found at meiotic prophase. From 2 to ± 30 pollen mother-cells may fuse, giving rise to large plasmodia. At metaphase I these syncytes behave as large cells, developing one bipolar spindle, on which all the bivalents present are arranged into one regular equatorial plate.

Svalöf, August 12th, 1940.

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THE CYTOLOGY OF THE SPECIES HYBRID ALLIUM CEPA × FISTULOSUM AND ITS POLYPLOID DERIVATIVES

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AMONG the species hybrids between *Allium Cepa* and *fistulosum* so far produced (EMSWELLER and JONES, 1935 b and c; LEVAN, 1936; MAEDA, 1937) there occur very marked cytological differences. My hybrid differs from the other hybrids in having decidedly more extensive irregularities during meiosis, and a more complete sterility. Although EMSWELLER and JONES (1938) found a common occurrence of fragments and chromatin bridges at meiosis in their hybrids, the general course of meiosis is comparatively regular. The chromosomes pair into 8 bivalents in 70 % of the cells and a trivalent association was found only once. MAEDA reports about the same frequency of complete bivalent pairing in his hybrid and no occurrence of higher associations than bivalents. EMSWELLER and JONES did not succeed in obtaining any F_2 generation after selfing of the hybrid, but several back-cross plants were secured. MAEDA obtained both a number of F_2 derivatives and some back-crosses with *Allium fistulosum*. My hybrid shows regular bivalent pairing in less than 2 % of the cells, all kinds of irregularities being common. In spite of many efforts to get back-crosses ever since 1936, I have failed to obtain a single germinating seed. On free flowering of the F_1 hybrid, however, each year a number of seed capsules swell up, about 10—15 in each inflorescence, and some of these give mature seed. These seeds originate from selfings or intercrossings among the 6 F_1 plants, which are cultivated in the same field plot. The parents are not cultivated within a distance of 400 m. The seeds are usually poor, but in 1938, however, 7 seeds germinated out of 48 seeds put to germination. The plants developing from these seeds constitute F_2 of the species cross. They flowered for the first time in the summer of 1939, but were not studied cytologically until this year, when 4 plants remained of the original 7.

The chromosome numbers of 6 of the plants are known, however, and all of them are higher than the diploid number (16), two are

triploids (24), 3 are hypo-tetraploids with 30 and 31 chromosomes, one is a pure tetraploid with 32 chromosomes. These conditions accentuate the difference between my F_1 hybrid and MAEDA's. All MAEDA's F_2 plants were normal diploids. After the thorough recasting, which the chromosomes of my hybrid are evidently subjected to during meiosis, it seems to be impossible to procure two gametes normal enough to form a viable diploid F_2 zygote. It is evidently easier for unreduced gametes to function, and such gametes were found to occur among the F_1 pollen in considerable frequency.

In the present paper the morphology and the cytology of the F_2 derivatives will be described. A supplementation of my earlier data on the cytology of the F_1 hybrid will also be given. The cytological technique described on earlier occasions has been used. The best pictures of meiosis are found in smear preparations fixed in BENDA—GEITLER according to the rapid method described by LEVAN (1937). As the somatic chromosomes of this cross have been treated previously (LEVAN, 1936), they will not be dealt with in this paper.

I. MORPHOLOGY OF THE CROSS.

The morphology of *Allium Cepa* and *fistulosum* as well as of their F_1 hybrid has been described by EMSWELLER and JONES (1935 b). My material agrees well with their description. The F_1 generation is perennial like the *fistulosum* parent, and the plants increase every year in viability. They are decidedly taller and stouter than *Allium Cepa*, which is the most vigorous parent. The inflorescences are spherical, as in *Cepa*, but larger, depending on the greater number of flowers present and the longer pedicels. Each flower is somewhat larger in the hybrid than in the parents, its shape is intermediate between that of the parents, although somewhat more similar to *Cepa*.

All the 4 surviving F_2 plants agree in habit with F_1, but they are even somewhat higher and stouter. The plant height in July 1940 was in the F_1 about 70 cm., in the tallest F_2 95 cm. The undoubtedly most robust plant was the triploid 1563—1. The shape of the inflorescences varies, while the triploids 1 and 2 are similar to the F_1 in type, although they have longer pedicels and a greater number of flowers, the tetraploid No. 4 has hemi-spherical inflorescences of a very characteristic appearance. The number of flowers is less than in F_1, the pedicels are somewhat arched and extremely coarse, being 1 mm. and more in diameter (Fig. 1 *k*). The pedicels have the same length, however, as in

Nos. 1 and 2, which makes the inflorescences appear almost sparse. The inflorescence of No. 6 (hypotetraploid) is spherical and is characterized by the pedicels being very much shorter than in the other F_2 plants (Fig. 1 *m*). This makes the inflorescences appear very dense.

The individual flowers of the F_2 plants are on an average larger than the F_1 flowers, with which they agree in type. No. 4 deviates somewhat, and resembles *Allium Cepa* in flower shape. Its flower shape is often even more expanded than that of *Allium Cepa*. It is the

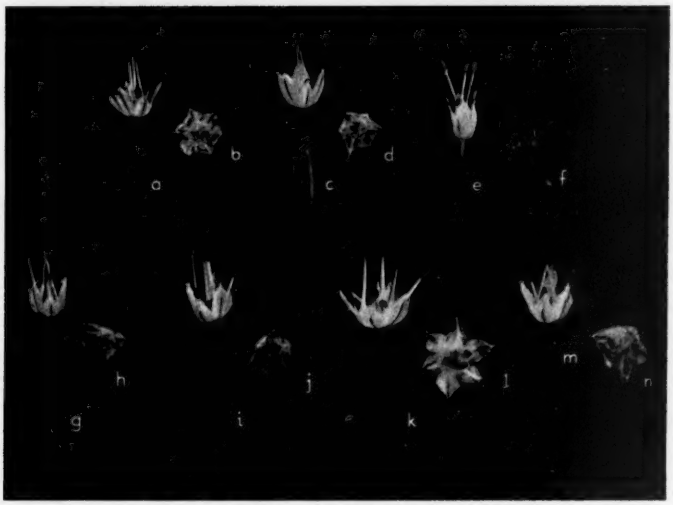

Fig. 1. Flowers of *a*, *b*: *Allium Cepa*, *e*, *f*: *Allium fistulosum*, *c*, *d*: the F_1 hybrid, *g*—*n*: 4 F_2 plants, *g*, *h*: 1563—1, *i*, *j*: 1563—2, *k*, *l*: 1563—4, *m*. *n*: 1563—6. — Photo. H. OLSSON, Svalöf.

largest of the F_2 flowers and has the appearance of a giant *A. Cepa* (compare Fig. 1 *a*, *b* with *k*, *l*).

The pollen fertility (Table 1), which in the *P*-generation is about 90—100 %, is in F_1 very poor, about 10 %. In F_2 the variation in pollen fertility is great: the two triploids 1 and 2 have a fertility similar to the F_1 and the same is true of the hypotetraploid 6. The tetraploid, 4, however, has a considerably increased pollen fertility, about 50—55 % good pollen. As will be shown later, the pollen fertility shows agreement with the course of meiosis in the different forms.

The cell-size of the pollen has been measured. Owing to a certain difference in shape between the pollen of *Cepa* and *fistulosum*, the

latter has a somewhat greater pollen-length. The F_1 varies very much in the shape of the pollen, but its pollen-length approximates that of the parents. The F_2 plants vary in pollen-length. No. 4, however, has a rather equal and regularly shaped pollen. All F_2 plants have a greater pollen-size than the diploids (Table 1).

The seed setting in the hybrid is, as already mentioned, extremely poor, and the few seeds secured are very different in shape and size. All the F_2 plants are seed-sterile. The different F_2 plants exhibit, however, very interesting differences in this respect. The triploids (1563—1, 2) are absolutely free from any seed setting, the flowers wither immediately after the florification. The hypo-tetraploid (1563—6) is characterized by the swelling of some seed capsules without any ripe

TABLE 1. *Pollen fertility and pollen length.*

Form	2n	Percentage good pollen		Length of the pollen in μ
		Before the first pollen division	Ripe pollen	
Allium Cepa	16	95,6	98,0	28,1
Allium fistulosum	16	89,6	89,2	31,4
F_1	16	15,2	11,6	30,5
F_2 1563—1	24	5,2	2,0	37,8
F_2 1563—2	24	18,4	12,0	37,3
F_2 1563—4	32	55,2	50,8	40,8
F_2 1563—6	31	18,8	12,8	34,7

seed being obtained. The tetraploid (1563—4) seems at first to be perfectly seed-fertile, the seed capsules of all flowers swell and form the normal number of seeds, which have been found to contain embryos. After some time, however, the seeds unfortunately begin to atrophy and almost all capsules are filled with a putrefying mass. At last only the dry black seed coats remain in the capsules. Evidently the development of the young embryos is interrupted at an early stage. One germinating seedling was secured, however, from the tetraploid.

II. MEIOSIS OF THE F_1 CROSS.

1. PACHYTENE.

The pachytene bivalents of certain Liliaceous plants have, as pointed out especially by HEILBORN (1939, 1940), a striking resemblance to the salivary gland chromosomes of the Diptera. Their interior

structure is, however, quantitatively different, since the salivary gland chromosomes, originated during a long resting stage associated with an immense increase in cellular volume, consist of a whole bundle of chromosome threads. Their band structure is caused by the presence of many homologous chromomeres at each level of the chromosomes. In the pachytene bivalents there is no such increase in the number of the threads. If the pachytene chromosomes are treated with fixing fluids containing a strong concentration of acetic acid and are then flattened out by mechanical pressure, the chromomeres will swell considerably into disciform bands, and owing to this increase in size of each chromomere differences in shape and size between the chromomeres will become exaggerated, which may be a help in mapping the chromosomes. After fixing in BENDA and in other fluids poor in acetic acid, we do not get these disciform bands, but dinstinctly punctiform chromomeres are seen all through pachytene. At early pachytene the chromomeres are smaller and less stainable, later on they grow in size and the distance between the chromomeres in the chromosome decreases. At the transition to diplotene, 4 chromomeres may be visible in each »band».

As already pointed out long ago by BELLING, among others, the chromomeres within a pachytene chromosome are morphologically different. These differences are readily distinguished in *Allium*, and have been pictured earlier. Since I considered it to be of interest to study once more pachytene of the F_1 hybrid *Cepa* × *fistulosum*, a rich material was fixed in modified FLEMMING, BENDA and NAVASHIN. These different fixatives turned out to be complementary to each other and gave a fairly reliable picture of the pairing conditions in F_1, although the pictures are, of course, not comparable to the clearness of salivary gland pictures.

There is a difference in the pairing present, depending on what stage of pachytene is examined. Earlier stages show a greater number of unpaired threads than later stages. In other words, zygotene has been extended. The maximal degree of pairing is found immediately before diplotene. It is then evident that the main part of the chromosome set has become paired. And the typical pairing is into bivalents. This indicates that the *Cepa* and *fistulosum* chromosomes are, generally speaking, homologous. As will be discussed later, there are certain signs, however, that not all pairing is between homologous threads.

It is impossible to analyse whole cells at pachytene. Certain bivalents may be followed, however, along their entire length. It is thus

seen that numerous unpaired regions occur in every cell. In the simplest case an unpaired loop is formed within otherwise completely paired bivalents. There may be evident morphological differences between the chromomeres of the two chromosomes within the unpaired loop, which may explain the missing attraction. On the other hand, it is often impossible to demonstrate any such morphological differences. Thus it cannot be decided in all cases whether the lack of pairing is caused by a structural difference between the chromosomes. On the other hand, sometimes very distinct differences of that kind

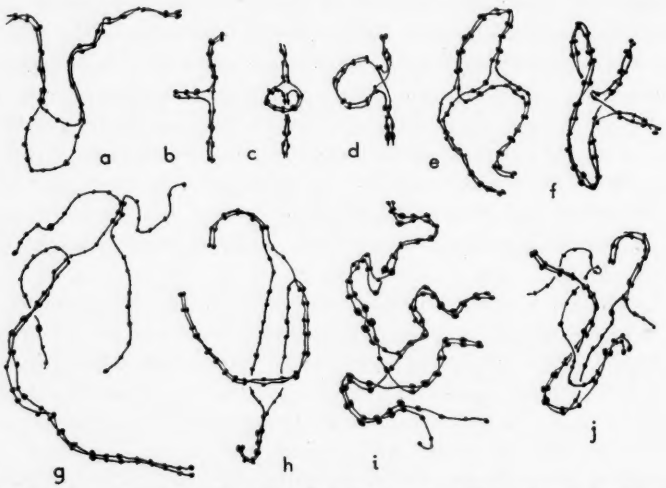

Fig. 2. Pachytene chromosomes of the F_1 hybrid, *a*, *b*: deficiencies, *c*—*f*: inversions, *g*—*j*: formation of multivalents. — × 3400.

do occur between intimately paired chromomeres. Thus one should be very cautious in drawing conclusions concerning the pairing homology of chromomeres from their morphological appearance.

On other occasions one thread is decidedly longer than the other within such a loop (Fig. 2 *a*), and in extreme cases the loop may be one-sided. In that case it may happen that the longer thread folds together and pairs with itself (Fig. 2 *b*). These one-sided loops are parallels of the deletions in the salivary gland chromosomes.

Another intra-chromosomal difference between *Cepa* and *fistulosum* is expressed in the formation of inversions, demonstrated both at pachytene and at metaphase—anaphase I. At pachytene exactly the same picture is encountered as that often figured in salivary chromo-

somes, viz. a ring-shaped loop (Fig. 2 *c*—*f*). This loop may vary greatly in size. It is easiest recognizable if it is not too large. The axis of the loop may be in the same plane as the bivalent (Fig. 2 *d*) or it may be turned transversally to it (Fig. 2 *c*). Since it is impossible, as already mentioned, to analyse whole cells, and since only the most clear inversions may be identified, I cannot form any opinion as to the frequency of the inversions. Probably particular conditions are necessary for the origin of these inversion loops, the short ones in particular may often form just an unpaired region of the bivalent. At metaphase and anaphase the inversions are very rare, which, however, is to be expected, since only those inversions can be detected within which a chiasma is formed.

Besides intra-chromosomal changes there are indications of inter-chromosomal differences. These result in the pairing of more than 2 chromosomes. Sometimes it is seen that this irregular pairing only involves a few chromomeres within one bivalent. These are then paired with a chromosome belonging to another bivalent. An instance of this is shown in Fig. 2 *g*. Such a small irregularity is frequently sufficient to considerably upset the pairing and it may result in long unpaired threads. Other pictures show a more regular trivalent pairing with the typical changes of pairing blocks. Fig. 2 *h* shows an irregular trivalent, which may form a ring at metaphase. More than three chromosomes may be involved in pairing. In Fig. 2 *i*, the normal picture of segmental interchange is found. This association was seen very seldom, and I am inclined to believe that only some of the paired chromomeres are really homologous. If such considerable lengths of 4 chromosomes were really homologous, this type of pairing should be met with very often, and at metaphase chains of 4 should be seen more often than is now the case. Other abnormal pairings are represented in Fig. 2 *j*.

These pachytene studies may be summarized thus: The chromosomes of *Allium Cepa* and *fistulosum* are generally speaking homologous, there is evidence, however, of both intra- and inter-chromosomal differences. As will be seen later, these conclusions agree with conditions in the amphidiploid, where, it is true, bivalents are ordinarily formed but where quadrivalents are by no means rare.

2. METAPHASE I.

In an earlier paper (LEVAN, 1936) I scrutinized metaphase I of the F_1 hybrid mainly by means of an analysis of the chiasma conditions

of 100 pollen mother-cells. It was found that the number of chiasmata per bivalent and per cell was considerably less, compared with *Allium Cepa*, the only parent which is comparable, since, as is well known, *Allium fistulosum* is characterized by chiasma localisation. While *Allium Cepa* has about 15 chiasmata per cell, the F_1 has only 8 chiasmata per cell. The typical bivalents of *Cepa* are rings with 2 chiasmata, while the F_1 usually has rod-shaped bivalents.

This scarcity of chiasmata in F_1 effects a regular occurrence of univalents. 8 bivalents per cell are very seldom formed in my hybrid. Thus, in LEVAN's 1936 paper complete bivalent pairing was found in 8 % of the cells, and in the hybrids examined later, complete bivalent formation was even rarer, in one case 4 such cells were counted among 250. In this respect my hybrid is the reverse of the other hybrids studied, as mentioned above.

In the present study I did not consider it worth while to add to the statistical material concerning chiasmata already collected within the hybrid. Instead I have examined purely qualitatively all pollen mother-cells at metaphase I of 12 slides from 6 flower buds. Instances of pairing anomalies, encountered during this work, and perhaps not sufficiently considered in my earlier paper, have been analysed.

The configurations of inversions will be dealt with first. As is often pictured they are at metaphase I characterized by one akinetic fragment and one chromatin bridge. In Fig. 3 *d*—*h* the 5 certain cases of inversion are pictured, which were found at metaphase I in the 6 flower buds investigated. Some more cases were observed, but they were considered uncertain or difficult to analyse. It should be noted that in 2 cases out of the 5 the s_1 bivalent (the satellited bivalent) is involved, the longer arm of which exhibits a rather long inversion fragment. The typical appearance of this bivalent is seen from Fig. 3 *a*—*c*, in the picture s_1f (*fistulosum*) is directed upwards and s_1c (*Cepa*) downwards. At metaphase I only the larger s_1f satellite is visible, while the small pointed s_1c satellite is completely embodied in the bulk of the chromosome. It may be concluded that in addition to the external differences between s_1c and s_1f, such as the different satellite shape, the different length relations of the chromosome arms etc., there also exists a structural difference, consisting of an inverted segment in about the middle of the longer arm. Judging from the relative rareness with which a chiasma is formed within the inverted region, this is probably rather small.

In the remaining 3 cases of inversions some of the longest two-

armed chromosomes are involved. In Fig. 3 *f* and *h* the fragment is rather long, in Fig. 3 *g* the fragment is smaller. This latter is the only ring-shaped bivalent observed with an inversion fragment. Fig. 3 *i*

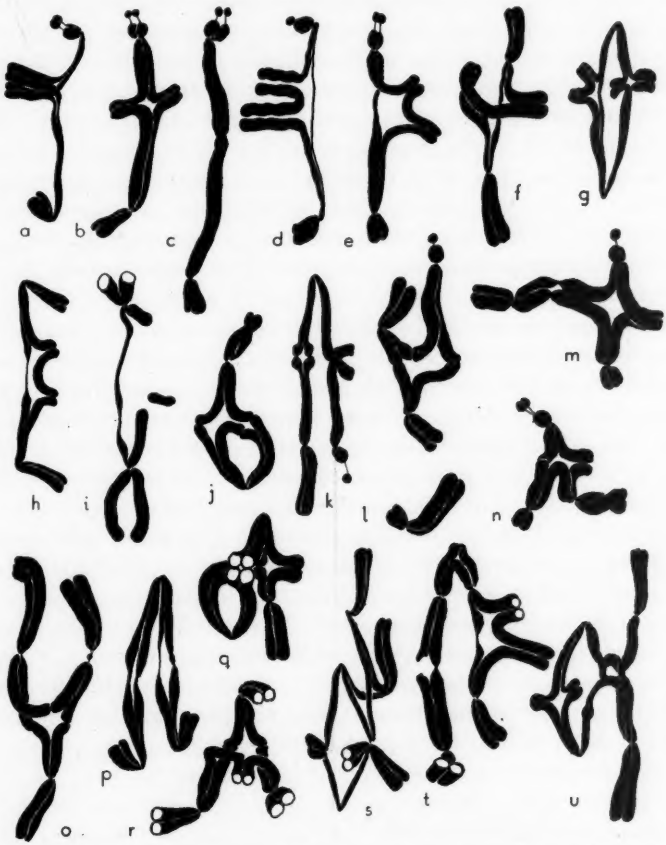

Fig. 3. Metaphase I of the F_1 hybrid, *a—c*: the s_1 bivalent, *d—e*: ditto with inversion fragment, *f—i*: other bivalents with inversion fragments, *j*: abnormal pairing in bivalent, *k—u*: multivalents. — × 2800.

shows a typical inversion bridge at anaphase I. These bridges are common at anaphase, and are probably formed also from other causes than inversions. EMSWELLER and JONES (1938) have discussed in some detail the occurrence of bridges and fragments in their hybrids.

The abnormal bivalent type represented in Fig. 3 *j* was reported

already in my earlier paper (LEVAN, 1936, Fig. 4 *p*). On that occasion it was noticed twice in 100 cells. I have now met with this configuration several times (15 times in 6 flower buds) and its appearance indicates that the same two chromosomes are concerned, which obtain this shape by means of a terminal chiasma formed between the one free arm and the other end of the same chromosome. STEBBINS (1938) found a similar configuration in the hybrid *Paeonia Delavayi* × *suffruticosa* and he gave two alternative explanations concerning its origin: »Either it is the result of a reduplication involving the two ends of the same chromosome, or of a long inversion involving the attachment constriction». (l. c. p. 99). The latter interpretation is considered the most probable one. This seems to be true also of *Allium*, as in the former case a ring-shaped univalent should be formed occasionally, but was never met with here.

Trivalents are not so infrequently formed. Also in this property my hybrid differs from the other hybrids. MAEDA did not observe any trivalent at all, and EMSWELLER and JONES came across only one trivalent joined with a triple chiasma among 232 cells investigated (l. c. 1938, Fig. 3 A). Earlier (LEVAN, 1936) I found as many as 14 trivalents in 100 cells. This high frequency of trivalents was not found this time. In all I found in the 12 slides investigated about 20 certain trivalents, but their real number is greater, as several more questionable trivalents were met with. I re-investigated my old slides from 1936 and checked their higher frequency of trivalents. As several of the 9 plants were investigated both in 1936 and now, the difference in trivalent formation observed must be due to modificative influences. It does not seem improbable that differences in the weather conditions, for instance, between the two occasions of fixing may have caused the observed difference in the frequency of trivalents.

The behaviour of the s_1 bivalent is of special interest. In no less than 4 cases it was found to form a trivalent with one of the long two-armed chromosomes (Fig. 3 *k*—*n*). Thus, in two cases s_1f was joined to this bivalent (Fig. 3 *k*, *l*), in one case forming a typical chain trivalent, in the other case forming a triple chiasma. In the other two cases s_1f and s_1c were joined to a two-armed chromosome by a triple chiasma (Fig. 3 *m*, *n*). Thus, a duplicated homologous piece of s_1f must occur in one or both chromosomes of another bivalent. Since s_1c was not seen to be paired with the two-armed chromosome, without forming a chiasma with s_1f as well, it cannot be decided whether this homologous piece is found also in s_1c. It may consequently be

postulated that in *Allium Cepa* a chromosome segment, which in *Allium fistulosum* is located in the satellite chromosome, is located in one of the two-armed chromosomes.

The commonest trivalent, which was met with in about 20 cells, was formed by exclusively two-armed chromosomes (Fig. 3 *o*—*s*). Although size differences occur between these chromosomes it could not be determined with certainty whether all these trivalents are built up from the same chromosomes. Pure chain trivalents (Fig. 3 *p*) were rarer than trivalents with a triple chiasma (Fig. 3 *o*, *r*). Ring and rod configurations, which need 3 chiasmata to be realized, were noticed only twice (Fig. 3 *q*, *s*). It is evident that small segments of the two-armed chromosomes are distributed on different chromosome pairs in *Allium Cepa* and *fistulosum*. These segments may influence the pachytene pairing, in which case such configurations as Fig. 2 *g* originate. If a chiasma is formed within these small segments a trivalent results. If chiasmata are formed also in other sections of the two chromosome pairs involved, a quadrivalent should originate. This occurs very seldom, however. On the earlier occasion (1936) I found 4 quadrivalents in 100 cells, but their frequency was very much less now. Only two certain quadrivalents were found (Fig. 3 *t*, *u*). One of these (Fig. 3 *t*) is a chain quadrivalent, which also contains a large inversion segment. The other (Fig. 3 *u*) consists of one ring and one rod bivalent joined by a quadruple chiasma. DARK (1936) finds a quadruple chiasma in *Paeonia Delavayi* and concludes that homologous end segments occur within two bivalents, »a condition which must have been brought about by the reduplication of two of these segments» (l. c. p. 365). As STEBBINS (l. c.) points out, these quadruple chiasmata do not necessarily indicate reduplications, small interstitially translocated segments may give the same effect.

III. MEIOSIS OF THE F_2 PLANTS.

Meiosis was studied in all the 4 F_2 plants flowering this summer. Among these the triploid (1563—2) and the tetraploid (1563—4) were investigated in some detail.

1. THE TRIPLOID F_2 PLANT 1563—2.

As expected, a great frequency of trivalents is found in the triploid. In polar view of metaphase I there were often counted 8 elements, most of them being trivalents, some, however, consisting of one bivalent and

one univalent lying close together. The number of univalents was determined in a number of cells:

Number of univalents	0	1	2	3	Total	Med.
Number of cases	8	31	15	4	58	1,3

In Fig. 4 *a—h* one metaphase plate has been analysed. All the chromosomes form trivalents, with the exception of s_1, which forms one bivalent, consisting of $s_1f + s_1c$ and one free s_1f chromosome. The presence of 2 s_1f and 1 s_1c in this plant was also verified in root cells.

The number of chiasmata in each trivalent is subject to considerable variation within each cell. This brings about a great diversity in the appearance of the different trivalents. See, for instance, Fig. 4 *a* and *h*, where *a* is a single chain trivalent with 2 chiasmata, *h* is a complicated trivalent with no less than 7 chiasmata. In 5 cells with complete trivalent formation the following numbers of chiasmata per trivalent were counted:

Number of chiasmata per trivalent	2	3	4	5	6	7	Total	Med.
Number of cases	10	18	8	2	1	1	40	3,2

The total numbers of chiasmata in each cell were 19/3, 25/3, 26/4, 29/3, 30/7, thus the variation in chiasma number was rather pronounced.

If the position of the chiasmata in the trivalents is studied, it may be seen that surprisingly few are really terminal. Instead a marked tendency to proximal chiasma localisation is observed, which results in the long side arms so often present (see, for instance, Fig. 4 *a—d, g*). So far no triploid species with strictly localized chiasmata has been described, but it may be concluded that localized trivalents should show features from the trivalents of 1563—2. Conditions of the tetraploid *Allium Porrum* with localized chiasmata (LEVAN, 1940) show that very few multivalents are to be expected in autopolyploid forms with proximal localisation of chiasmata.

It seems that the same situation is present in this triploid F_2 plant of *Cepa* × *fistulosum* as MAEDA describes in the diploid F_2 plants studied by him, viz. the simultaneous occurrence of both localized and random chiasmata in the same individual and even in the same cell.

The only trivalent which can be identified in every cell is the s_1 trivalent. Some instances of this trivalent are pictured in Fig. 4 *i—n*. The satellites of the two s_1f chromosomes are nearly always visible, while the satellite of s_1c is never seen. Usually two of the chromosomes are more intimately joined, while the third chromosome may be attached to them by a terminal chiasma or be entirely free. s_1f is intimately joined to the other s_1f about as frequently as to s_1c.

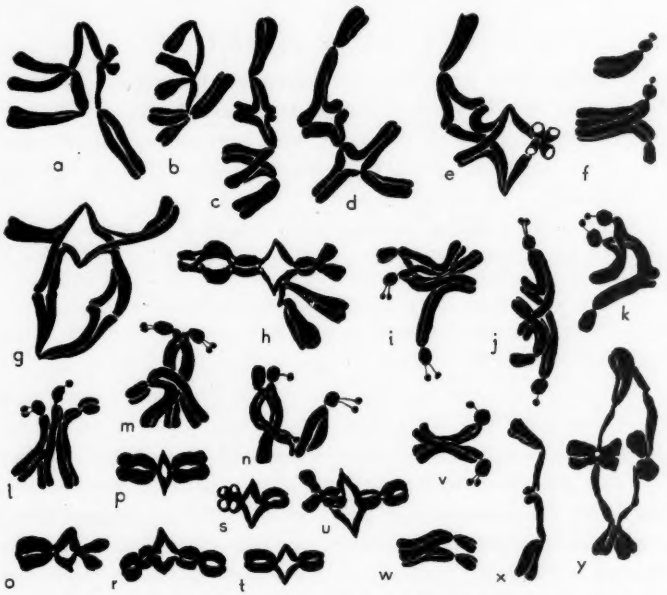

Fig. 4. Metaphase I of two F_2 plants, *a—n*: the triploid 1563—2, *o—y*: the amphidiploid 1563—4. — × 2750.

Since abnormalities in the pairing, such as inversion fragments and chromatid asymmetry, are, as shown above, very frequent in the F_1 hybrid, similar abnormalities should be expected also in the F_2 triploid. This is also the case. As the cells of the triploid are difficult to analyse completely, I have not been able to estimate their frequency. Fig. 4 *c* gives an example of an asymmetric chiasma.

Frequent disturbances occur at anaphase and telophase I. In late telophase I the following frequency of micro-nuclei and chromatin bridges were counted:

Normal cells	1 micro-nucleus	2 micro-nuclei	3 micro-nuclei
51	18	5	1

1 micro-nucleus + 1 bridge	2 micro-nuclei + 2 bridges	Total
6	1	82

2. THE TETRAPLOID F_2 PLANT 1563–4.

The commonest occurring configuration in meiosis of the tetraploid F_2 plant is the typical *Allium* bivalent, the ring bivalent with side-arms. Also rod bivalents occur, although more seldom. In some cells even 16 bivalents could be counted, indicating that the form in reality constitutes an amphidiploid.

It is of great interest to study the chiasma conditions of the bivalents. 50 bivalents selected at random had the following number of chiasmata:

Number of chiasmata	1	2	3	4	5	6	7	Total	Med.
Number of cases	2	9	12	13	8	5	1	50	3,7

As appears, the variation is rather wide, from 1 to 7 chiasmata being found. Fig. 4 *o*—*x* show instances of bivalents from the amphidiploid. The bivalents are symmetric and normal. It is evident that their pairing is autosyndetic, *fistulosum* pairing with *fistulosum* chromosomes and *Cepa* with *Cepa*. In the case of the s_1 bivalents this condition may be observed directly (Fig. 4 *v*, *w*).

The number of chiasmata per bivalent is rather high, on an average about 4. In *Allium Cepa*, the only comparable species of the parents, the corresponding number is 1,9 and in F_1 0,9. In this F_2 amphidiploid an entirely new situation is present, the random distribution of the *Cepa* parent dominates in the same manner as in F_1, and contrary to the conditions in F_1 every chromosome in the amphidiploid has an exactly homologous partner, allowing maximal bivalent pairing. The frequency of chiasmata must then be determined by an interaction of the genotypic tendencies to chiasma formation of the *Cepa* and *fistulosum* genomes. Although the tendency of chiasma formation in *Allium fistulosum* is concealed by the localisation, which brings about

a constant frequency of 2 chiasmata per bivalent, it is quite possible that the species has a high genotypic tendency to chiasma formation.

Although bivalents are the most frequent configurations in the amphidiploids, univalents and quadrivalents are also found. In 40 cells the following 8 types of configuration were noted:

		1	2	3	4	5	6	7	8
Type of configuration	I	0	0	0	1	1	2	2	2
	II	16	14	12	14	12	15	13	11
	III	0	0	0	1	1	0	0	0
	IV	0	1	2	0	1	0	1	2
Number of cells		13	8	4	4	5	3	2	1

It must be mentioned, however, that only the more schematic configurations are possible to analyse, so this table gives a somewhat simplified picture of the situation.

The quadrivalents (Fig. 4 *y*) have the ordinary *Allium* type, chains, rings and more complicated configurations. As seldom more than 2 quadrivalents per cell were observed, it may be concluded that the frequency of quadrivalents is less in this amphidiploid than in autotetraploid species, which was also to be expected.

Anaphase I is rather regular, often 16 chromosomes could be counted at each pole. Now and then, however, laggards were seen and also inversion bridges, which were evidently caused by incidental allosyndetic pairing. The meiotic irregularities were not great enough, however, to explain the total seed sterility of the form. The high fertility of the pollen as well as the incipient development of numerous embryos go to show that the sterility of this amphidiploid is not haplontic but diplontic.

IV. DISCUSSION.

The species hybrid *Allium fistulosum* × *Cepa*, the cytology of which is described in the preceding chapters, exhibits certain features which are of special interest. The differences in cytological behaviour between the hybrids so far produced indicate the presence of genetically and structurally different races within the two parental species. As has already been pointed out, the hybrids of EMSWELLER and JONES and of MAEDA show a more regular course of the entire meiosis than

my hybrid. It may consequently be assumed that the races of *Allium fistulosum* and *Cepa* used by these authors are more closely related than the parental forms used by the present writer. During my stay at Beltsville in 1937 I had the opportunity of studying the meiotic slides from the different hybrids produced by EMSWELLER and JONES, and I was then able without difficulty to notice that the general appearance of meiosis in their hybrids was quite different from meiosis in my material. The differences were too great to be explained merely as modifications caused by environmental factors, even if the culture conditions in Maryland are very much different from those in South Sweden. It should be mentioned that in MAEDA's hybrid as well as in at least some of EMSWELLER and JONES's hybrids the same variety of *Allium Cepa* was used, viz. Yellow Danvers, which in both cases was crossed with Japanese forms of *Allium fistulosum* (»Nebuka» in one case and »Hidanegi» in the other). In my hybrid an entirely different material was used, viz. the known commercial variety »Braunschweiger» of *Allium Cepa* and a form of *Allium fistulosum* from a European botanic garden.

The differences in the behaviour of the hybrids are very evident already in the cytology of the F_1 but they become even more striking if the chromosome numbers of the F_2 generation are considered. In the present case exclusively polyploids were obtained, while in the other cases no polyploids at all appeared. The greater and more profound changes, which the chromosomes of my hybrid are exposed to during meiosis of the F_1, bring about a considerable gametic sterility and render the surviving gametes incapable of producing viable diploid progeny. Only if more than two genomes fuse can the defects present be covered. Thus 2 triploids and 4 $\pm$ tetraploids were formed. From earlier results in *Allium Schoenoprasum*, *paniculatum* and *nutans* it is well known that gametes with a doubled chromosome number may function not so infrequently. Usually a doubled ♀-gamete fuses with a normal ♂-gamete, but also doubled ♂-gametes may function.

Three of the F_2 plants died during the first winter, but the remaining 4 have a very good vitality. The tetraploid, 1563—4, is morphologically intermediate between the parents, though with some preponderance towards *Allium Cepa*. The occasional complete pairing into 16 bivalents indicates that this form, although originated by gametic doubling, constitutes a clear amphidiploid built up from 2 *Cepa* and 2 *fistulosum* genomes. DARLINGTON put forward his rule concerning the behaviour of polyploids already in 1929. According

to this rule a doubled species hybrid obtains a greater fertility the greater the sterility of the primary hybrid. This rule has proved to be generally valid, the hybrid *Cepa* × *fistulosum* is an exception, which may be said to confirm the rule. The amphidiploid is, it is true, almost completely seed sterile (one living progeny plant was obtained from 5 inflorescences), but this sterility is due to specific conditions. It is clearly not gametic since a complete embryo formation is present. The development of the embryos is interrupted, however, at a rather advanced stage, when already all seed capsules have swollen up and assumed a fertile appearance. The difference in behaviour of the F_1 hybrid is striking. The F_1 lacks in most flowers every sign of seed setting. In the amphidiploid, on the other hand, the constitution of the gametes evidently forms no obstacle to a complete seed setting. Then at a rather late stage some physiological factors evidently turn up and interrupt the further development of the seeds. These factors may be sought for in the interaction between the mother plant and the seed. The one seed which I have succeeded in bringing to development has given rise to a strong and vital plant, indicating that the obstacle to the development of the progeny is not of a genotypical kind.

The cross between *Allium Cepa* and *fistulosum* is of special interest since it constitutes the first and as yet the only cross between forms with random chiasmata and with strictly proximal chiasma localisation. In all cases where the F_1 hybrid has been produced and investigated cytologically, the normal chiasma distribution has dominated. Unfortunately the hybrid turned out to be so sterile that very few F_2 plants or back-crosses have been obtained. MAEDA obtained 13 F_2 plants, 9 of which had exclusively random chiasmata while 4 showed preponderating random chiasmata together with 2 or 3 localized bivalents per cell. In the back-crosses by MAEDA there occurred 21 plants, 6 of which had normal bivalents and 15 of which contained 1—4 localized bivalents. EMSWELLER and JONES (1934) obtained 17 back-cross plants, 10 of which were normal while 7 had localized bivalents. EMSWELLER and JONES have very kindly furnished me with the results they obtained in the study of numerous progenies from different F_1 hybrids produced after the publication of their papers 1935 a, b, c. In their material, too, many plants occurred with both random and localized chiasmata in the same cell.

The F_2 derivatives dealt with in the present paper are on account of their polyploidy not strictly comparable with the derivatives earlier described. It is clear, however, that random distribution of the

chiasmata predominates in my F_2 plants as well as in F_1. In the amphidiploid and still more in the triploid F_2 plants the chiasma distribution exhibits markedly more variable conditions than are met with in a pure species of *Allium*, e. g. *Allium Cepa*. Although random chiasmata prevail frequent localized chiasmata are found in the triploids. The variation in chiasma frequency is also greater than normally. There is no doubt that the balance in chiasma formation is upset in some way or other.

DARLINGTON (1939 a and b) discusses the conditions existing during the chiasma formation. He sets up a number of »independent variables of meiosis», the variation of which governs the numerous different types of meiosis met with in nature. The localisation of chiasmata is, according to DARLINGTON, a meiosis type which especially organisms with long chromosomes are apt to acquire, since the chromosome pairing in such organisms tends to be interrupted before pairing is complete. Now if forms with differently adapted meiotic types are crossed, the meiotic mechanism will be upset and result in unbalanced chiasma conditions: »The same exact adaptation and buffering of the meiotic mechanism is revealed by the variety of disordered types that are produced in the second generation when two differently adjusted species are crossed» (DARLINGTON, 1939 a, p. 68).

According to this view, the irregularities of the chiasma formation in F_2 and in back-crosses of the *Cepa* × *fistulosum* cross are due to the occurrence of recombination types with unbalanced chiasma conditions, types which under natural conditions would soon be exterminated. Thus, each bivalent of an individual has no special tendency to assume the one type or the other, but owing to an unbalanced genotype in this respect a lack of co-ordination during the chiasma formation causes strictly localized chiasmata to be formed at the same time and in the same nucleus as random chiasmata. The triploid F_2 plants of the present investigation show a chiasma distribution which is in accordance with this view, most trivalents having exclusively random chiasmata, while a varying number of localized chiasmata occur in different cells. MAEDA's observations are not consistent, however, with this view. In his material the same bivalent type always showed the same type of chiasmata.

It would no doubt be of great interest if a greater number of tetraploid derivatives from this cross was produced. By selection of types with many localized chiasmata it should be possible to arrive at a tetraploid *Cepa* × *fistulosum* with strict chiasma localisation. One

tetraploid species with exclusively localized chiasmata is known (*Allium Porrum*; LEVAN, 1940), and its meiosis proved to be remarkably regular, quadrivalents being extremely rare. By utilisation of such a property as chiasma localisation it may thus be possible to obtain a decidedly greater stability than is ever found in a polyploid form with ordinary random chiasmata, where even in an amphidiploid, such as *Cepa* × *fistulosum*, quadrivalents are formed not so infrequently. It may be mentioned in conclusion that this autumn some 30 seeds of the primary hybrid have been brought to germination. A preliminary test of their chromosome numbers shows that the majority of these plants are tetraploids. For the further study of the problems touched upon in this paper a larger material will therefore be available.

SUMMARY.

The hybrid *Allium Cepa* × *fistulosum* has yielded a progeny of 7 F_2 plants. The chromosome number is known in 6 of them, all being polyploids (2 plants are triploids and 4 plants are quasi-tetraploids). The morphology and meiotic behaviour of F_1 and F_2 are described. Structural irregularities such as deficiencies, inversions and multivalent formation are studied at pachytene and metaphase I of the F_1. Meiosis of one triploid and one tetraploid F_2 plant is followed in some detail. The 32-chromosome F_2 plant sometimes forms 16 bivalents and is thus considered to be an amphidiploid. A comparison is made with the behaviour of earlier produced hybrids between *Allium Cepa* and *fistulosum*. The quality of chiasma localisation is discussed.

Svalöf, October 23rd, 1940.

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CHROMOSOMAL ABERRATIONS IN RYE POPULATIONS

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I. INTRODUCTION.

THE work reported in the present paper was undertaken on account of some results obtained in the genus *Galeopsis*. Pure lines of *Galeopsis Tetrahit* frequently give partially sterile F_1 hybrids, and this sterility and the accompanying meiotic irregularities were shown to be due to structural chromosome differences between the lines (MÜNTZING, 1938). In the same paper and in a more recent review (MÜNTZING, 1939) other cases of structural chromosome differentiation in autogamous species were discussed. It was also inferred that in allogamous populations heterozygosity for structural chromosome differences must be rather frequent. This, indeed, has already been demonstrated in *Drosophila* (cf. DOBZHANSKY, 1939 and MÜNTZING, 1939, p. 346), mainly thanks to the salivary gland chromosomes.

In plants the occurrence of heterozygosity for segmental interchange, inversions, duplications and deficiencies, should be apparent by partial sterility, especially on the male side. Therefore pollen quality in a number of diploid, auto- as well as allogamous, species was studied. The results obtained (cf. MÜNTZING, 1939, Tabelle 1) really demonstrated a quite clear average difference between the two categories. The self-fertilizing species had all very good pollen, in contrast to most of the cross-breeding species, which were found to include a considerable proportion of more or less sterile individuals. This was also found to be true of rye, which is a strictly allogamous species. According to the table cited (MÜNTZING, 1939, p. 336), not less than 50 per cent of the 610 rye plants examined at that time were partially sterile, having more than 10 per cent shrivelled pollen grains (cf. l. c., Fig. 1). Among these plants, which were ordinary population plants, the percentage of good pollen was in fact found to cover the whole range from 0 to approximately 100 per cent good pollen.

According to the theory this pollen sterility should be due to heterozygosity for structural chromosome differences. The validity

of this idea might be tested by cytological studies, and since rye is a rather favourable cytological material, such studies were concentrated on this species. The idea was to study in the first place the meiotic conditions as well as fertility and viability in a sufficient number of population plants of rye and later on to continue with a collection of inbred lines. In the present paper our report will be limited to a number of cytological aberrations occurring in ordinary population plants of the species.

The meiotic divisions were studied in altogether 167 population plants of rye, belonging to the varieties »Stålråg» and »Östgöta Gråråg». The latter variety is characterized by a rather poor percentage of seed-setting and was therefore supposed to be an especially favourable material for the study undertaken. However, meiosis in both varieties was found to be more regular than expected. Nevertheless a number of aberrations were duly discovered (cf. Table 1, p. 298). Of the 167 plants examined 98 were found to be quite regular, 53 showed slight irregularities of various kinds while inversions were observed in 5 plants and segmental interchange in 6. Finally, 3 plants had extra chromosomes or fragments, one plant showed cytomixis, and one plant was a tetraploid-diploid chimæra. It should also be mentioned that one of the plants representing a segmental interchange was also found to be heterozygous for an inversion, and that a plant with $2n = 14 + 2$ f showed cytomixis in some cells.

All these individuals were either taken directly in the rye populations or belonged to progenies raised from single open-pollinated population plants (cf. Table 1). The fixations of the p. m. c. were made in diluted chrome-acetic-formalin and the sections stained with gentian violet, these methods generally giving rather good results.

II. CYTOLOGICAL RESULTS.

1. REGULAR BEHAVIOUR AND SLIGHT IRREGULARITIES.

In most of the plants reported to be regular first metaphase and first anaphase were studied. In a minority of cases the plants were considered to be regular from studies of diakinesis or first metaphase only. The slight irregularities observed belonged to different categories. The most frequent deviation was the occurrence of non-conjunction. Univalents in various frequencies were observed in 25 plants. No detailed frequency counts had so far been undertaken, but it was rather obvious that different plants represented different degrees of non-

conjunction. In a further 28 plants various other slight irregularities were observed, especially difficulties of separation at I—A, sometimes followed by fragmentation. Figs. 1—2 represent two I—A groups of this kind from the same plant. The anaphase groups all contain 7 chromosomes, but from these some fragments have obviously been detached. The plant in question did not otherwise carry any fragments but had $2n = 14$.

In plants with difficulties of separation at I—A the chromosomes were often rather elongated and narrow and at least in some cases had a relatively low chiasma frequency. In other plants, on the contrary, the chromosomes at I—M were highly contracted.

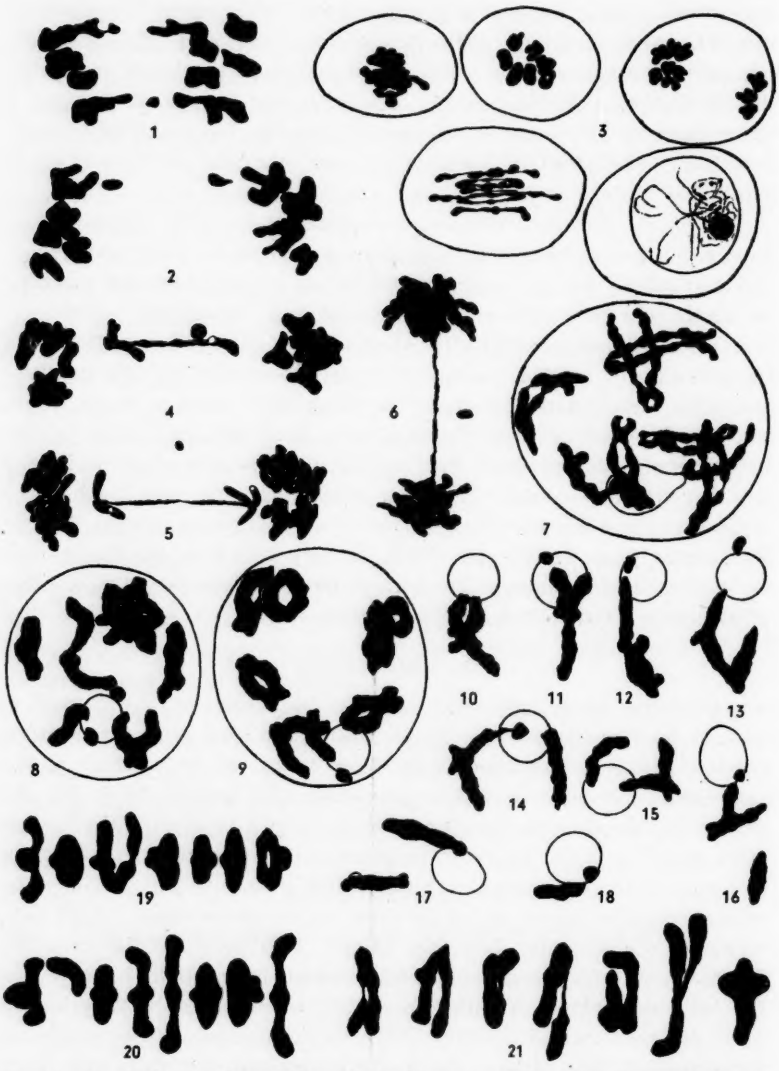
Another observation worthy of mention is that pollen mother cells lying free in the loculi or being only poorly in contact with the tapetum generally represented less advanced stages than those p. m. c. which were in close contact with the tapetum. Such detached cells, though not otherwise degenerated, had not in most cases passed pachytene or other prophase stages. In a few cases such cells had reached the I—M stage, but the chromosomes were much less contracted than in the regular p. m. c. (Fig. 3). This strongly indicates that the meiotic cycle is not autonomous in the p. m. c. but is influenced by substances produced or transmitted by the tapetum.

2. INVERSIONS.

Dicentric chromatids and acentric fragments were observed at I—A or I—T in five plants. Three cells of this kind from three different individuals are represented in Figs. 4—6. Another figure of the same kind has been published previously (MÜNTZING, 1939, Fig. 4). Of the figures given in the present paper Fig. 4 represents the earliest stage and Fig. 6 the latest. The position of the centromeres and the different chromosome arms are particularly clear in Fig. 5. The size of the fragment seems to be different in the three cases. As a rule, however, the fragment is rather small. This fact and the very low frequency of true chromosome bridges in all these plants indicate that the inverted sections are small and that, on an average, they have a more or less terminal position in the chromosomes. If the inversions were median, large fragments would be formed.

3. TRISOMIC PLANTS.

Two sister individuals in the progeny from an open-pollinated population plant were both found to have an extra chromosome. No



Figs. 1—21. Meiosis in population plants of rye. — Figs. 1—2, fragmentation at I—A due to difficulties of separation; Fig. 1, seven chromosomes in each anaphase group, one free fragment and one almost detached fragment; Fig. 2, as Fig. 1 but two free fragments. — Fig. 3, five adjacent p. m. c. in natural position showing different stages of development and contraction. The 3 cells in the upper row (2 I—M groups and 1 incomplete I—A) are in close contact with the tapetum.

other plants in this progeny were examined cytologically. The chromosome behaviour of both these plants was found to be quite identical. At first the extra chromosome, which is frequently unpaired, was supposed to be a large fragment, but after a more detailed study it seems more probable that the plants were ordinary $2n + 1$ individuals. A study of diakinesis revealed that the extra chromosome and its homologues were the SAT-chromosomes and thus involved in the development of the nucleolus.

At diakinesis or late diplotene the SAT-chromosomes were observed in 71 more or less completely analysed cells. In 29 cells these chromosomes formed a trivalent, which is attached to the nucleolus either with one or two of the chromosomes, in the remaining 42 cells the SAT-chromosomes were present as bivalent + univalent. In 19 of these cases both the bivalent and the univalent were in touch with the nucleolus, in 17 cells only the bivalent, and in 6 cells only the univalent. These conditions are illustrated in Figs. 7—18. Fig. 7 represents a complete nucleus at early diakinesis with $7_{II} + 1_{I}$. One bivalent and the univalent are attached to the nucleolus. Fig. 8 is a complete nucleus at diakinesis showing just the same configuration. In Fig. 9, on the other hand, the configuration is $I_{III} + 6_{II}$. In the trivalent only one satellite is visible. In Figs. 10—18 the different relations between the SAT-chromosomes and the nucleolus are further elucidated. In Figs. 10—13 these chromosomes are present as a trivalent, having two (Figs. 10—11) or only one chromosome (Figs. 12—13) in touch with the nucleolus. In Fig. 13 the satellite is widely separated by the nucleolus from the rest of the chromosome. A similar, though less extreme, situation is met with in several of the other cases represented in Figs. 7—18. On the other hand, clear satellites were not observed on SAT-chromosomes which were free from the nucleolus. In Figs. 14—15 the satellite chromosomes form a bivalent and a univalent, both of which are attached to the nucleolus, the bivalent, however, with one arm only. Figs. 16—17 also show nuclei with II + I, but of these only the bivalent is attached to the nucleolus. In Fig. 16 the nucleolus is formed in cooperation with only one SAT-chromosome. This chromosome is a member of a bivalent, the third chromosome lying as a uni-

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The 2 lower cells are not in touch with the tapetum. Of these the cell to the left has very elongated and chiefly rod-shaped chromosomes, the cell to the right is still in prophase. — Figs. 4—6. Evidence of inversions in three different plants. Dicentric chromatids and fragments at I—A and I—T. — Figs. 7—21, meiosis in a trisomic plant. — Fig. 7, early diakinesis, complete nucleus with $7_{II} + 1_{I}$; Figs. 8—9, diakinesis nuclei with $7_{II} + 1_{I}$ and $6_{II} + 1_{III}$ respectively; Figs. 10—18, the relation between the nucleolus and the three satellite chromosomes; Figs. 10—11, trivalent with two of the chromosomes in touch with the nucleolus; Figs. 12—13, trivalent with only one chromosome in touch with the nucleolus; Figs. 14—15, bivalent + univalent, both in touch with the nucleolus; Fig. 16, bivalent + univalent, only one of the chromosomes in the bivalent in touch with the nucleolus; Fig. 17, bivalent + univalent, a small extra nucleolus is formed at the univalent; Fig. 18, the nucleolus is only associated with one SAT-univalent. Figs. 19—20, I—M groups (separately drawn) with $1_{III} + 6_{II}$ and $7_{II} + 1_{I}$ respectively. Figs. 21, separate I—M trivalents. — Fig. 3, × 1065, all the other figures, × 2130.

valent at some distance from the nucleolus. In Fig. 17 there is also a SAT-bivalent attached to the nucleolus and a free univalent. It is interesting to note, however, that this free univalent has been able to form a small nucleolus of is own. This was also observed in another cell. Fig. 18, finally, represents the last category, in which the nucleolus is only associated with one SAT-univalent, the corresponding bivalent being free. Thus, it seems that as a rule all three SAT-chromosomes are not involved in the formation of the nucleolus but only one or two.

At first metaphase the extra chromosome was present as a univalent in the majority of the cells. Of 51 completely analysed I—M groups 15 had the configuration $I_{III} + 6_{II}$, as in Fig. 19, the remaining 36 cells showing $7_{II} + 1_{I}$. A I—M group with the latter configuration is represented in Fig. 20 and a number of separate trivalents in Fig. 21. The high frequency of univalents as compared with trivalents suggests that the extra chromosome might be a large fragment. However, the shape of the trivalents does not confirm this view. At any rate, the three chromosomes constituting the trivalents seem to be exactly or approximately equal in size.

The frequency of trivalents was found to be somewhat higher at diakinesis than at first metaphase, the percentage values being $40{,}80 \pm 5{,}83$ and $29{,}4 \pm 6{,}38$ respectively. The difference, however, is not significant.

At first anaphase the extra chromosome was sometimes included in one of the daughter nuclei without division (observed in 12 cells), but sometimes it was found to split at the equator (observed in 15 cells).

4. A PLANT WITH TWO SMALL EXTRA CHROMOSOMES.

A single plant of the variety »Östgöta Gråråg» was found to have 16 instead of 14 chromosomes. The two extra chromosomes were distinctly smaller than the ordinary chromosomes and could be recognized at meiosis without difficulty. This was especially easy, as in most p. m. c. they appeared as univalents. Such is the case in Figs. 22 and 23, representing I—M groups with $7_{II} + 2$ f in side view and polar view. The same configuration has evidently characterized the commencing anaphase shown in Fig. 24.

In a minority of cases the two small chromosomes formed an extra small bivalent, as demonstrated by Fig. 25 and Fig. 26 (third bivalent from the right). When forming a bivalent the small chromosomes were almost always united by one terminal chiasma. Only in one single instance was the chiasma observed to be interstitial (Fig. 26 *b*).

Counts of the frequency of paired and unpaired fragments were made in 3 different slides. In slide No. 1, 84 p. m. c. at I—M showed the following configurations:

Configuration:	8_{II};	$7_{II} + 2$ f;	$6_{II} + 2_{I} + 2$ f;	$5_{II} + 4_{I} + 2$ f.
Number of cells:	16 ;	64 ;	3 ;	1
Per cent:	19,0;	76,2 ;	3,6 ;	1,2

According to these values the occurrence of two unpaired fragments is the rule, such cells being about four times as frequent as those with paired fragments. In a few cells real univalents may occur besides the fragments.

However, as all the I—M groups were not clear enough to be analysed, it is possible that the true percentage of cells with 8_{II} is slightly higher, such configurations being somewhat more difficult to distinguish than those with $7_{II} + 2$ f. This is indicated by counts of the number of free fragments in cells which were not otherwise analysed. Such counts were undertaken in slide No. 1 and in two further slides, the following results being obtained:

	Number of cells with			Percentage of cells
	0	1	2 fragments	with 0 fragments
Slide No. 1	45	4	106	29,0
» » 2	29	5	98	22,0
» » 3	66	10	125	32,8
Total	140	19	329	28,7

In all three slides the percentage of cells without visible fragments is higher than the percentage of cells in slide No. 1, observed to have 8_{II}. The differences, however, are not significant. At any rate, it may be concluded that in this plant *at least two thirds of the p. m. c. contain I—M groups with unpaired fragment chromosomes.*

The behaviour of the extra chromosomes at I—A is partly illustrated by Figs. 27—29. In Fig. 27 the anaphase distribution is 7—2—7, the lagging univalents being undivided. In Fig. 28 one of the univalents has almost reached the pole and will certainly be included in one of the interphase nuclei. The other univalent, on the contrary, has divided and, consequently, the distribution corresponds to 8—2/2—7. In Fig. 29, finally, both the univalents have divided and approach the other anaphase chromosomes.

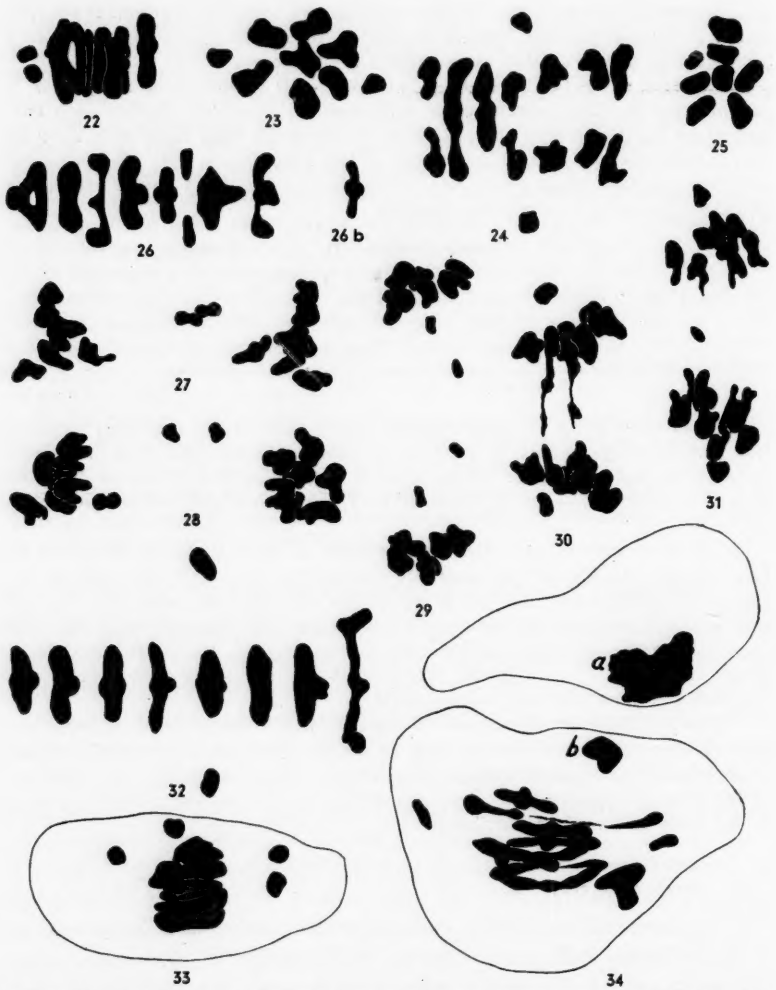
However, random distribution or regular disjunction of the fragments was found to be more frequent than division. In a total of 65 cells 41 showed no division, 14 division of one fragment and 10 cells division of both fragments. The behaviour of the extra chromosomes was further elucidated by the following observations as to the mode of anaphase distribution:

Distribution:	8—8;	7—2—7;	7—1—2/2—7;	7—4/2—7;	7—2/2—8
Number of cells:	25	11	10	5	2

According to these values the gametes will have a very good chance of receiving 8 chromosomes, though a certain amount of elimination will occur.

5. CYTOMIXIS AND BINUCLEATE POLLEN MOTHER CELLS.

Besides the rather regular meiotic behaviour described above in the plant with 16 chromosomes some special irregularities were observed in the same plant. Fragmentation, following difficulties of separation at I—A, is illustrated in Figs. 30—31. This phenomenon, however, has already been described above for other plants. Much



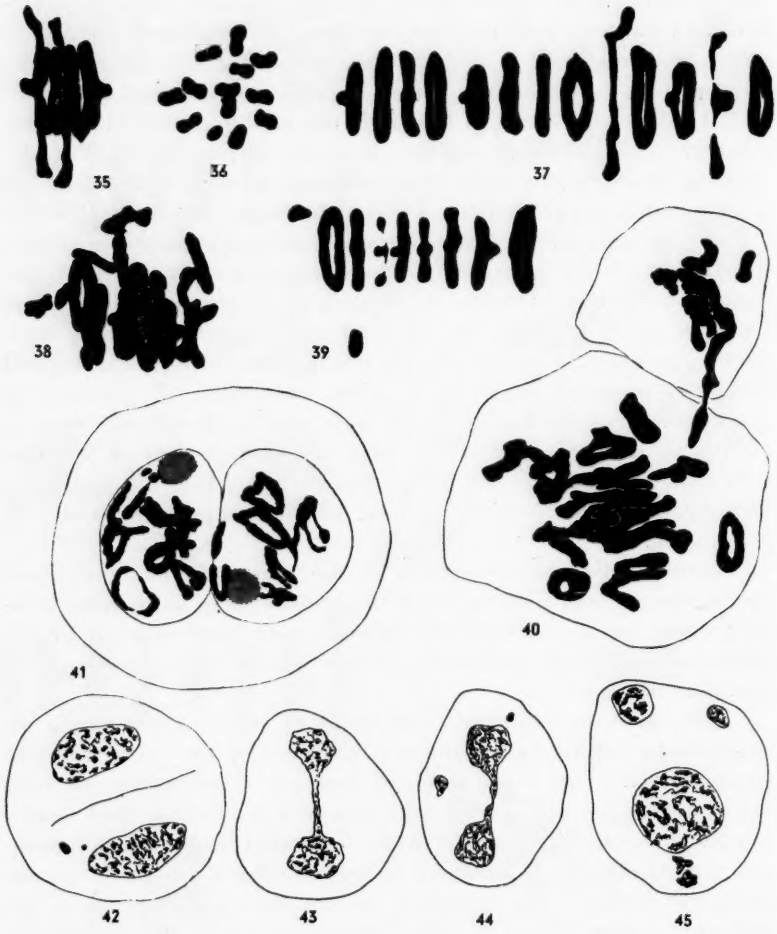
Figs. 22—34. Meiosis in a plant with two small extra chromosomes. — Figs. 22—24, $7_{II} + 2$ f; Fig. 22, I—M in side view, Fig. 23, I—M in polar view, Fig. 24, commencing anaphase (almost natural position); Figs. 25—26, 8_{II}, Fig. 25, polar view, the small extra rod-bivalent clearly visible, Fig. 26, side view (separately drawn), the small extra bivalent is the 3rd from the right; Fig. 26 *b*, an exceptional small bivalent with interstitial chiasma; Figs. 27—29, I—A, Fig. 27, distribution 7—2—7, Fig. 28, one of the small lagging chromosomes has divided, the other is near one of the anaphase groups, Fig. 29, both lagging chromosomes have divided, distribution 7—4/2—7. Figs. 30—31, fragmentation at I—A due to difficulties of separation,

more remarkable is *the occurrence of pollen mother cells with supernumerary bivalents and fragment chromosomes.* The first observation of this kind was a I—M group clearly containing $8_{II} + 2$ f (Fig. 32). Another p. m. c. of otherwise normal appearance was found to contain $9_{II} + 4$ f (Fig. 33). Six other cells were observed to deviate in a similar manner. This peculiar variation is partly explained by Fig. 34, showing two adjacent cells at first metaphase. In one of the cells there is only a large, irregular lump of chromatin (*a*), in the other cell, close to the large lump in the first cell, there is a smaller body of a similar structure (*b*), which seems to have been detached from *a* at an earlier stage. The body *b* probably corresponds to a bivalent. In the same cell there are 8 other bivalents and 2 fragment chromosomes. Thus, the increased number of elements in this cell and the others mentioned has, most probably, arisen by so-called cytomixis. The increase in chromosome number has probably, as a rule, occurred later than at pachytene, since no multivalents were observed in most of the cells with supernumerary chromosomes. Only in one cell of this kind were there two probable trivalents, the total complement probably consisting of $2_{III} + 6_{II}$.

Corresponding to the cells with too many chromosomes there should also be cells with less than 16 chromosomes. Such cells, however, could not be distinguished with certainty from cells cut by the microtome knife and containing a lower number of chromosomes for that reason.

Cytomixis in the plant with $2n = 14 + 2$ f (*R. 42*) might be supposed to be due to a disturbing influence of the extra fragment chromosomes. This is not the case, however, since similar and even more pronounced phenomena were observed in another plant having exactly $2n = 14$. In this plant (*R. 697*) cytomixis and related phenomena were found to be frequent in one slide and especially in one particular anther. The conditions in this slide are reflected by the following figures (Figs. 35—45). In several loculi ± tetraploid cells were quite frequent; they never occurred alone, however, but were mixed with ordinary diploid cells, showing 7 bivalents at first metaphase. Such a normal cell is represented in Fig. 35. In Figs. 36—38 the metaphase groups are approximately tetraploid. In Fig. 36

otherwise distribution 8—8 (the small chromosomes may be recognized at the poles). Figs. 32—34, exceptional cells with supernumerary chromosomes due to »cytomixis»; Fig. 32, $8_{II} + 2_I$, Fig. 33, $9_{II} + 4_I$, Fig. 34, two adjacent cells, the body *b* (probably a bivalent) in the lower cell seems to have been detached from the now irregular chromatin mass *a* in the upper cell, in the lower cell a total of $9_{II} + 2_I$. — × 2130.



Figs. 35—45. Cytomixis in an otherwise normal plant with $2n = 14$. — Fig. 35, a normal I—M group with 7_{II}; Figs. 36—38, approximately tetraploid I—M groups, Fig. 36, polar view, 13_{II}, Fig. 37, side view (separately drawn), also 13_{II}, Fig. 38, $10—11_{II}$, the other chromosomes unpaired; Fig. 39, a cell intermediate between diploidy and tetraploidy, $8_{II} + 2_{I}$, the third bivalent from the left very small; Fig. 40, two cells connected by chromosome elements, due to premeiotic irregularities, the lower cell ± tetraploid; Fig. 41, a binucleate p. m. c. at diakinesis (the cell will certainly give a tetraploid I—M group); Figs. 42—45, interphase, Fig. 42, normal, Figs. 43—45, various irregularities. — × 2130 (Figs. 35—41) and × 1600 (Figs. 42—45).

(polar view) there are probably 13 bivalents, and the same number of bivalents could clearly be distinguished in another cell seen in side view (Fig. 37). Fig. 38 shows the natural position of the bivalents and univalents in another approximately tetraploid cell. Cells with chromosome numbers intermediate between 14 and 28 were also observed. The cell represented in Fig. 39 was found to contain $8_{II} + 2_{I}$. One of the bivalents (third from the left) was remarkably small, but quite clear.

That these apparent cytomixis phenomena are in reality due to premeiotic irregularities sometimes combined with fusion of nuclei at the transition between diakinesis and first metaphase is rather clear from Figs. 40—41. In Fig. 40 a chromosome belonging to a probable bivalent seems to have penetrated the cell walls and connects two different cells. The chromosome number in the smaller cell could not be distinguished, but in the larger cell there are at least 28 chromosomes, or probably a somewhat higher number. Since the sum of the chromosomes in the two cells under consideration is obviously higher than 28, it is not possible that the tetraploid cells in this case and the others arise in such a way that the chromosomes of one diploid cell are actively pushed into another diploid cell. The true explanation must be premeiotic irregularities of mitosis leading to binucleate pollen mother cells or pairs of cells connected by strands of incompletely separated chromosomes. The cells shown in Fig. 40 are probably the result of disturbances of both these kinds. — A single binucleate pollen mother cell was actually observed (Fig. 41). The nuclei represent the diakinesis stage and lie in close contact. At first metaphase such a cell will certainly appear to be tetraploid, combining all the chromosomes into one metaphase group.

In the slide under discussion tetraploidy was only observed at first metaphase, all more advanced stages showing the normal chromosome number. Thus, in this case the aberrant cells do not seem to be able to compete with those representing a regular chromosome behaviour. The last traces of previous irregularities were seen at interphase. Fig. 42 represents a normal interphase while Figs. 43—45 show various irregularities which ultimately must be due to premeiotic disturbances.

Finally, it should be mentioned that the irregularities in plant *R. 697* were chiefly observed in one of five slides examined. The other four slides showed an almost or quite normal chromosome behaviour. Hence the irregularities described must be due to rather localized,

probably physiological, disturbances. Extreme irregularities of a similar kind were observed by LEVAN (1941) in haploid *Phleum pratense*.

6. SEGMENTAL INTERCHANGE.

Evidence of segmental interchange between non-homologous chromosomes was obtained in three unrelated population plants. In one of these plants the inheritance of the structural deviation was also studied in two successive generations (Types *a* and *b*).

TYPE *a*.

Among the population plants fixed in 1937 there was one individual (*R. 525*) which was characterized by the I—M configuration $1_{IV} + 5_{II}$. This plant was briefly mentioned in a previous paper by MÜNTZING (1939, p. 338) and a typical I—M group was reproduced (l. c., Fig. 3). A further study of this plant showed that the occurrence of one quadrivalent [1] per metaphase group was almost quite regular. Of 25 cells examined 24 had $1_{IV} + 5_{II}$, and only one cell was found to contain 7 bivalents. The associations of four chromosomes were sometimes straight rings, and in such cases very easily distinguishable, but more frequently the rings were zig-zag-arranged. Chains of four chromosomes instead of rings were also observed. Fixation in this case was not sufficiently good to permit a detailed study. However, in the next generation, obtained after open pollination of the mother plant, plants with associations of four chromosomes were again met with. In one of these plants (*R. 111*) fixation proved to be rathed good. This allowed a more detailed study of meiosis, which gave the following results.

Of 30 cells at *diplotene* or early diakinesis 29 were found to contain $1_{IV} + 5_{II}$, as in Figs. 46—47, and only in one cell there were 7_{II}. Of the 29 quadrivalents 22 were closed rings and 7 were chain-shaped. In the quadrivalents the chromosomes seem to represent four different sizes, the largest chromosome (No. 1) being one and a half or almost twice as long as the smallest one (No. 4) (Figs. 46—53). In cells with chains of four instead of closed rings the opening is in most cases caused by lack of chiasmata between the shortest chromosome and one of its partial homologues. Such cases are represented in Figs. 47—48 and 50. If the ring is closed the shortest chromosome is almost regularly connected with one of the other chromosomes by a single terminal or subterminal chiasma (Figs. 51—53). For the further identification of the chromosomes a knob-like structure, often visible

[1] For the sake of simplicity the term »quadrivalent» is used instead of »associations of four chromosomes» or »amphibivalent» which might be more adequate.

at the homologous ends of the two longest chromosomes, seems to be of use (Figs. 46 and 49—50). With the aid of the size relations and this knob the four different chromosomes in the quadrivalents, indicated by 1—4, could be identified with more or less certainty. Fig. 51, for instance, seems to represent a typical case. These observations led to a tentative diagram (Fig. 54), illustrating our opinion as to the relative size of the chromosomes and the exchanged segments in the quadrivalent.

At *first metaphase* the configuration was found to be $1_{IV} + 5_{II}$ in 33 cells and probably 7_{II} in one cell. The 33 quadrivalents belonged to four different categories, viz. 15 zig-zag rings, 2 non-zig-zag rings, 13 zig-zag chains and 3 non-zig-zag chains. In order to get more reliable values as to the frequencies in these four categories, quadrivalents from 76 additional cells were studied. If these data are added to those just mentioned the result will be the following total values:

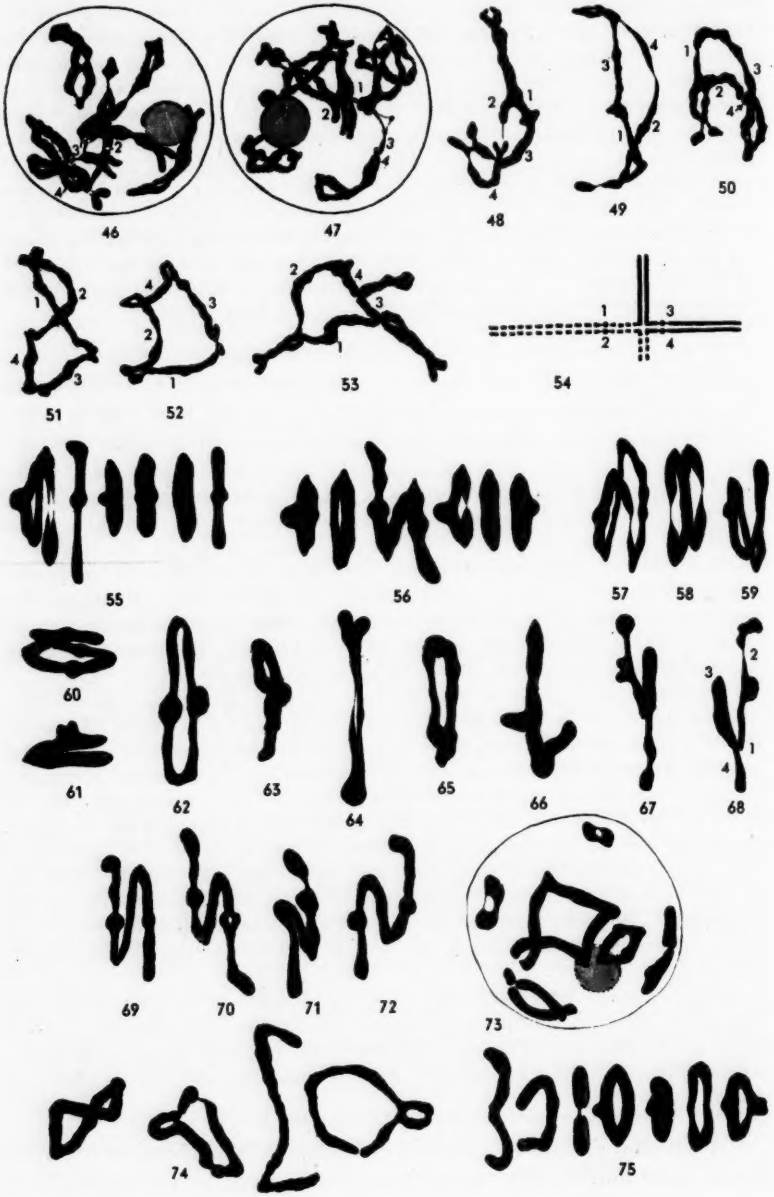
	Zig-zag	Non-zig-zag	Total
Chains	34	11	45
Rings	56	8	64
	Total 90	19	109

Zig-zag-arrangement is obviously much more frequent than the opposite alternative, and rings are probably more numerous than chains. The percentage values will be $58{,}7 \pm 4{,}7$ for rings and $41{,}3 \pm 4{,}7$ for chains. In reality the rings were probably still more frequent, the zig-zag rings being more difficult to distinguish than the chains.

The appearance of the I—M chromosomes is shown in Figs. 55—72. Figs. 55 and 56 represent two complete groups with $1_{IV} + 5_{II}$. In the former group the quadrivalent is a zig-zag ring, in the latter group a zig-zag chain. Figs. 57—61 show separate quadrivalents of the most frequent type, the zig-zag ring. In Figs. 57—60 probably all the chromosomes are united by single terminal or subterminal chiasmata. Fig. 61 represents a more exceptional case, in which two of the chromosomes are united either by one interstitial chiasma or possibly by two chiasmata. The same thing is true of the quadrivalent in Fig. 55. Two non-zig-zag rings are shown in Figs. 62—63 and two chains of a similar type in Figs. 64—65. As before, several, but not all, chromosomes are united by single, terminal or subterminal chiasmata. Figs. 66—72, finally, show the appearance of a number of zig-zag chains. On an average, terminalisation seems to be less complete in the chains than in the rings. However, there are no specially conspicuous chiasmata even in the chains, in contrast to the conditions met with in another translocation heterozygote (Type *c*).

Since clear size differences between the chromosomes in the quadrivalent were observed at diplotene, attempts were made to identify the individual chromosomes also at I—M. However, as the exact position of the chiasmata in the I—M quadrivalents could not always be localized, these attempts did not lead to quite convincing results.

Additional evidence on meiosis in »Type *a*» was obtained from the plants *R. 62* and *R. 139*. Both these plants were grand-daughters of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R. 525, the meiosis of which was described above. In *R. 62* only diakinesis stages were available. Twenty-five cells, in which the total chromosome complement could be distinguished, all had $1_{IV} + 5_{II}$. A cell of this kind is represented in Fig. 73, and 4 single quadrivalents in Fig. 74. The quadrivalent in Fig. 73 seems to be composed of chromosomes of different sizes. Most chiasmata in this quadrivalent and the others are terminal or subterminal. In *R. 139* some observations on I—M groups could be made. Of 33 cells analysed 26 had $1_{IV} + 5_{II}$, the remaining 7 cells containing 7_{II}. In the cells of the latter kind at least two of the bivalents were rod-shaped. A cell of this kind is shown in Fig. 75. The two bivalents to the left certainly represent the four chromosomes that usually form a ring. The bivalents in question are slightly asymmetrical and do not look like ordinary rod bivalents. All the other bivalents are rings of the usual type.

TYPE *b*.

The plant *R. 525*, its daughter *R. 111* and grand-daughters *R. 62* and *R. 139* all show a meiosis of the same type and are characterized by the configuration $1_{IV} + 5_{II}$ (Type *a*). Greatly to our surprise another daughter plant of *R. 525* was found to have $2_{IV} + 3_{II}$ quite regularly. This new plant, *R. 193*, described below as Type *b*, was obtained after open pollination of the mother plant in the same manner as the sister plant *R. 111*.

The appearance of first metaphase in *R. 193* is evident from Figs. 76—79, all showing $2_{IV} + 3_{II}$. In Fig. 76 both quadrivalents are straight, non-zig-zag rings, in Fig. 77 one quadrivalent is of the same type and the other one zig-zag-arranged. In Fig. 78 both quadrivalents are of the latter kind. In Fig. 79, finally, representing a group in polar view, there is one zig-zag ring and one non-zig-zag chain.

Two slides of this plant were good enough to permit counts of configurations, types of quadrivalents and chromosome distribution at I—A.

Figs. 46—75. Segmental interchange, Type *a*. — Figs. 46—53, late diplotene; Figs. 46—47, two complete nuclei with $1_{IV} + 5_{II}$; Figs. 48—53, separate associations of four chromosomes; the chromosomes indicated by 1—4 in the various associations in Figs. 46—53 probably correspond to each other; Fig. 54, a tentative diagram, indicating the size relations and the points of interchange in the quadrivalent association; Figs. 55—56 two complete I—M groups (separately drawn), $1_{IV} + 5_{II}$; Figs. 57—72, separate quadrivalents of different types; Figs. 57—61, zig-zag rings; Figs. 62—63, non-zig-zag rings; Figs. 64—65 non-zig-zag chains; Figs. 66—72, zig-zag chains; Fig. 73, diakinesis with $1_{IV} + 5_{II}$; Fig. 74, four separate quadrivalents at diakinesis; Fig. 75, a I—M group with 7_{II}, the two open bivalents to the left certainly represent the chromosomes usually forming a quadrivalent. — × 2130.

In the first slide 55 I—M groups were analysed, and of these 4 had $1_{IV} + 5_{II}$, all the other 51 showing $2_{IV} + 3_{II}$. In the second slide the corresponding figures were 1 and 24. Added together, this implies that *of the 80 cells studied 75, or 94 per cent, had* $2_{IV} + 3_{II}$.

The type of quadrivalent was recorded in 105 cases, the result being the following:

	Zig-zag	Non-zig-zag
Ring:	59	41
Chain:	3	2

As in Type *a*, zig-zag arrangement is evidently more frequent than the opposite, and the preponderance of rings over chains is even more pronounced than in Type *a*.

In the majority of cases chromosome disjunction at I—A proved to be regular. In 15 cells both the anaphase groups had 7 chromosomes, and in 5 additional single anaphase groups the chromosome number was the same. — Exactly the same situation was met with at *second metaphase*. Of 28 cells, in which both II—M plates could be counted, 26 had the distribution 7 + 7, and only 2 cells had 8 chromosomes in one plate and 6 in the other. Similarly, 30 out of 31 single II—M plates had 7 chromosomes, and only in one plate 8 chromosomes were observed.

Thus, although more than half of the chromosomes in this plant are members of quadrivalents the great majority of the gametes will evidently receive 7 chromosomes.

TYPE *c*.

A case of segmental interchange distinctly different from Types *a* and *b* was observed in the plant *R. 712*. Though belonging to the same variety, »Stålråg», this plant is not related at all to the plants representing Types *a* and *b*.

At early diakinesis the cells were regularly found to contain five bivalents and an association of four chromosomes. The appearance of this quadrivalent is shown in Figs. 80—89. It may be compared with the Type *a*-quadrivalents represented in Figs. 46—53. Though Figs. 80—89 show a somewhat later stage than Figs. 46—53 it is rather obvious that the present case of interchange is different from the preceding one. In Type *a* size differences between the chromosomes in the quadrivalent were obvious (cf. Figs. 46—53), but such differences are not so clear in the present case. Moreover, the quadrivalents of plant *R. 712* often gave the impression of being composed of two distinct pairs (cf. Fig. 82), the size of the segments exchanged consequently being rather small. However, the four chromosomes at this stage in most cases formed a closed ring, which was only broken occasionally (Fig. 89).

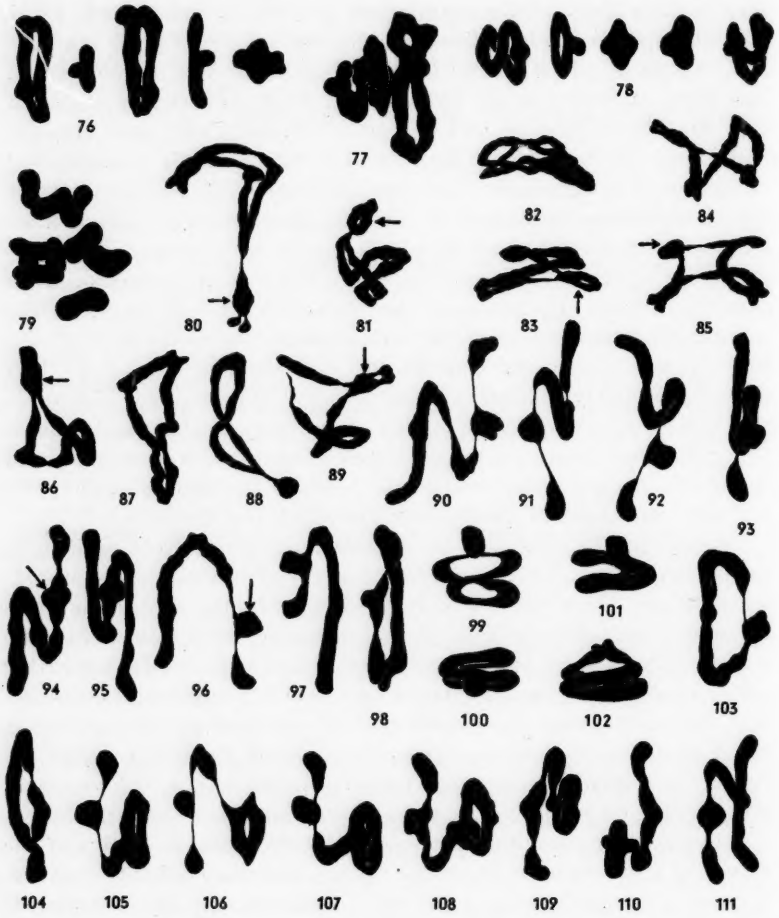
The difference between the present case and Type *a* became quite

clear from a study of the associations at *first metaphase*. In plant *R. 712* the quadrivalents at this stage are characterized by the presence of a large lump of chromatin between two of the four chromosomes. This lump, indicated by an arrow in Fig. 96, is also clearly visible in Figs. 90—93, 97, 99—101, 103 and 105—108. It is also quite characteristic that the connections between the lump and the neighbouring chromosomes are generally quite thin and narrow. The true nature of this characteristic formation is not quite clear, but evidently it must contain an interstitial chiasma, which cannot be terminalized. Probably there are two chiasmata, one interstitial and one terminal. In a minority of cases (19,6 per cent) this lump was replaced by the rather sharply circumscribed structure indicated by an arrow in Fig. 94, which is also present in Figs. 95, 98, 102, 104 and 109—110. This structure probably indicates one subterminal chiasma, and sometimes two free ends are visible (Fig. 102). In every quadrivalent studied either the large lump or this subterminal chiasma was present, and apparently there were no transitions between the two categories. At any rate, classification hardly ever presented any difficulty.

Evidently the structures in question have also a fixed position in the quadrivalents. This is evident from the chains and ring-and-rod-quadrivalents (Figs. 90—98 and 105—109). In the chains the lump or subterminal chiasma was situated between one terminal and one median chromosome, the terminal chromosome, as a rule, appearing rather small. Only one exception to this rule was observed. In Fig. 95 it is conceivable that an original ring of four has opened out into a chain in a different manner from that usually occurring. — In the ring-and-rod-quadrivalents the lump or subterminal chiasma was always situated in the rod, separating its two chromosomes.

Further it is clear that the lump (of both types) is always of the same, or approximately the same, size. This would imply that the narrow, attenuated parts of the two chromosomes always represent the same region. It is probably this region that is visible already at diakinesis as a marked constriction or rather as a thin thread separating a small part of the quadrivalent association from the rest (indicated by an arrow in Figs. 80, 81, 83, 85, 86 and 89). The true nature of this region is not clear, but probably it represents some kind of structural differentiation. Similar pictures have been observed also in a certain line of inbred rye and from this material more complete information may be gathered.

As may be seen by comparing the I—M quadrivalents of Types *a*



Figs. 76—79. Segmental interchange, Type *b*, I—M groups with $2_{IV} + 3_{II}$. — In Fig. 76 (side view, separately drawn) both quadrivalents are non-zig-zag rings, in Fig. 77 (side view, natural position) there are one zig-zag and one non-zig-zag ring, in Fig. 78 (side view, separately drawn) both quadrivalents are zig-zag rings, and in Fig. 79 (polar view) there is one ring and one chain. — Figs. 80—111, segmental interchange, Type *c*. Figs. 80—89, separate quadrivalents from early diakinesis (the arrow in Figs. 80—81, 83, 85, 86 and 89 indicates the structure, which probably corresponds to the large I—M lump in Fig. 90 etc.); Figs. 90—111, separate I—M quadrivalents of different types; Figs. 90—95, zig-zag chains; Figs. 97—98, non-zig-zag chains; Figs. 99—102, zig-zag rings; Figs. 103—104, non-zig-zag rings; Figs. 105—110, ring-and-rod quadrivalents; Fig. 111, a quadrivalent of the type ¦, - -.

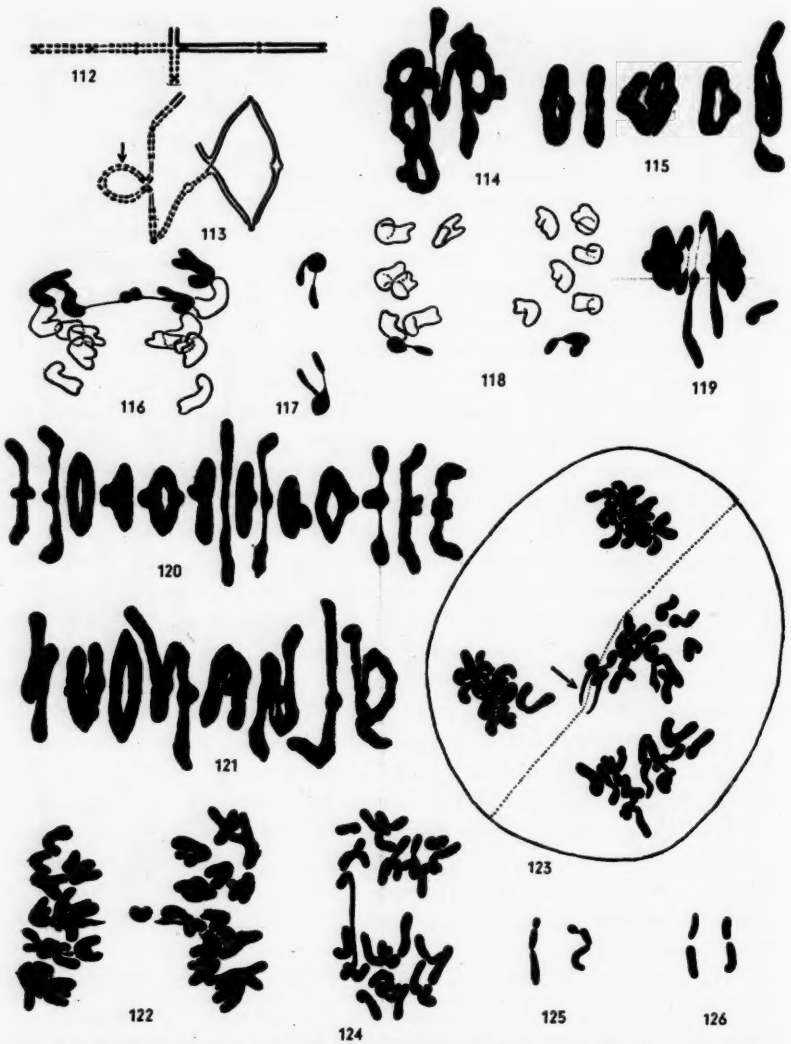
and *c*, the characteristic localized chromatin lumps are not present in the Type *a* plants (cf. Figs. 55—72). A difference between the segmental interchanges of Types *a* and *c* is not only demonstrated by the above data but also by the relative frequencies of rings and chains. At I—M closed ring quadrivalents were found to be less frequent in Type *c* than in Type *a*. In the present case (Type *c*) the kind of quadrivalent was determined in a total of 243 cells, belonging to two different slides. The percentage of ring quadrivalents was found to be $40{,}1 \pm 3{,}8$ in the first slide and $27{,}6 \pm 5{,}1$ in the second. Since the difference is not significant, the values from the two slides may be added. This gives a total percentage of $36{,}2 \pm 3{,}1$ for Type *c*. In Type *a* the *minimum* frequency of rings was found to be $58{,}7 \pm 4{,}7$ per cent. The difference between these values, $22{,}5 \pm 5{,}6$, is significant. Thus, Type *a* is characterized by a higher frequency of ring quadrivalents at first metaphase than Type *c*.

In Type *c* six different types of quadrivalents could be distinguished. The most frequent category was the zig-zag chain (Figs. 90—95), which occurred in $34{,}6 \pm 3{,}1$ per cent of the 243 cells observed. Next in frequency were the zig-zag rings ($28{,}8 \pm 2{,}9$ per cent, Figs. 99—102) and the ring-and-rod-quadrivalents ($18{,}9 \pm 2{,}5$ per cent, Figs. 105—110). Of the remaining categories, non-zig-zag chains (Figs. 96—98) were most frequent ($9{,}5 \pm 1{,}9$ per cent). Non-zig-zag rings (Figs. 103—104) occurred in $7{,}4 \pm 1{,}7$ per cent of the cells, and, finally, quadrivalents of the type shown in Fig. 111 were seen in two cells ($0{,}8 \pm 0{,}6$ per cent).

It is a striking fact that ring-and-rod-quadrivalents were rather frequent in Type *c*, occurring in $18{,}9 \pm 2{,}5$ per cent of the cells, and almost completely absent in the Type *a* and *b* plants. A quadrivalent of this type was only observed once in *R. 139* (Type *a*) and was not seen at all in the plant representing Type *b*. This fact, which emphasizes still more strongly the difference between Type *c* and the previous cases of segmental interchange, may be explained by a tentative diagram (Figs. 112—113).

According to this diagram the ring is formed by two chromosomes that are largely homologous and have large homologous sections on both sides of the centromere. The other two chromosomes have probably arms of different lengths, the large, conspicuous chromosome lump (indicated by an arrow) or the corresponding structure being formed

The arrow in Fig. 96 indicates the large chromatin lump typical of Type *c* quadrivalents. In some cases this lump is replaced by the structure indicated by an arrow in Fig. 94. — × 2130.



Figs. 112—118. Segmental interchange in Type *c* (continued). — Fig. 112, a tentative diagram indicating the size relationships and the points of interchange of the chromosomes at pachytene in the quadrivalent. This diagram is based on the associations observed at early diakinesis (cf. Figs. 80—89) and at I—M. Fig. 113, a diagram indicating the probable constitution of the ring-and-rod quadrivalents (Figs. 105—110). As indicated in Fig. 112, the large chromatin lump is supposed to be formed by two chiasmata at the same side of the centromere in one of the large homologous

by chiasmata in the longer arm which has no interchanged segment. According to this diagram the ring should have one short free arm. This arm is more or less clearly visible in Figs. 107—108 and 110—111.

It remains to report that in Type *c*, just as in Types *a* and *b*, cells without a quadrivalent were quite rare. The chromosome configuration was counted in a total of 180 I—M groups, and in 176 of these the configuration was found to be $1_{IV} + 5_{II}$, as in Fig. 114. In two exceptional cells there were probably 7_{II} and in a few other of the 176 cells it was not quite certain, whether four of the chromosomes, counted as quadrivalents, were not really two separate bivalents. — In the third of the 4 exceptional cells the configuration was $1_{III} + 1_{I} + + 5_{II}$, and in the fourth it was clearly $2_{IV} + 3_{II}$ (Fig. 115). The latter cell indicates that segmental interchange has also occurred between other non-homologous chromosomes than those involved in the regularly occurring quadrivalent. This second interchange, however, must involve rather small segments, as only one cell out of 180 gave evidence of such an interchange. It is also possible that the occurrence of a second quadrivalent is due to a new interchange, which has occurred in a cell of this plant shortly before meiosis.

At *first anaphase* typical dicentric chromatids and fragments were seen in some cells (Fig. 5), thus demonstrating that the plant in question was not only heterozygous for a segmental interchange but also for an inversion. It is tempting to assume that this inversion may have something to do with the localized or non-terminalized chiasma

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regions. In the other large homologous region a ring is formed by chiasmata on both sides of the centromere; Fig. 114, a complete I—M group (in almost natural position) with $1_{IV} + 5_{II}$; Fig. 115, an exceptional I—M group (separately drawn) with $2_{IV} + 3_{II}$; Figs. 116—118, I—A; Fig. 116, the black chromosomes are certainly previous members of the quadrivalent, the chromosomes forming the large lump separating with difficulty. The corresponding chromosomes are also represented in Fig. 117 and Fig. 118 (the black chromosomes). — Fig. 119. Segmental interchange in Type *d*. I—M group with $1_{III} + 1_{I} + 5_{II}$. — Figs. 120—126. Meiosis in a tetraploid spike of the diploid-tetraploid chimæra. Figs. 120—121, I—M groups with 14_{II} and $6_{IV} + 2_{II}$ respectively; Fig. 122, I—A group showing the distribution 14—14 but with an additional large fragment and probably a dicentric chromatid; Fig. 123, II—A, a dicentric chromatid (indicated by the arrow) has been eliminated at the first division; Fig. 124, II—A with the distribution 13—13 and in addition a dicentric chromatid stretched between the poles; Figs. 125—126, corresponding pairs of lagging chromosomes in the two II—A groups of two different p. m. c. The laggards in the same p. m. c. (resulting from division of one chromosome at I—A) have the same morphology, but laggards from different p. m. c. may be different (two constrictions in Fig. 125, one in Fig. 126). — × 2130.

in the quadrivalent, but there is no direct evidence for such an assumption. Thus, the inversion may just as well be situated in one of the bivalents.

It was observed, however, that the chromosomes forming the large chromatin lump in the quadrivalent separate with difficulty at I—A. This is evident from Fig. 116 in which the four black chromosomes certainly are previous members of the quadrivalent. The separation of the chromosomes involved in the chromatin lump is further shown in Figs. 117—118. Apart from this difficulty of separation, disjunction and chromosome distribution at I—A were rather regular. The distribution 7—7 was observed in several cells.

TYPE *d*.

It was just mentioned above that in Type *c* one exceptional cell showed $2_{IV} + 3_{II}$ instead of $1_{IV} + 5_{II}$, the regular association in this plant. A corresponding observation was made in the plant *R. 696*. This plant had a regular meiosis with 7_{II} at first metaphase. However, one single but quite clearly deviating I—M group was observed (Fig. 119), this group showing $1_{III} + 1_{I} + 5_{II}$. This strongly indicates that the plant, or possibly a local sector, was heterozygous for an exchange of some rather small segments of non-homologous chromosomes. At any rate, if chiasma formation is between homologous segments, one of the chromosomes in the trivalent must be partially homologous with the other two.

7. A DIPLOID-TETRAPLOID CHIMÆRA.

Before making fixations of meiosis in rye the correct stage of the spikes was always tested with aceto-carmin. During work of this kind in 1938 an entirely tetraploid spike on a plant belonging to the variety »Östgöta Gråråg» was detected. A closer study of this plant revealed that it was a diploid-tetraploid chimæra. The spike fixed belonged to the youngest tiller of the plant. As soon as the tetraploidy of this tiller had been observed the plant in the field was closely studied. It was found to carry five tillers, two of which had already flowered, one having almost finished flowering but having some fresh anthers left, and two tillers which had not yet flowered. On the spikes which had already flowered, the kernels produced were taken care of, on the other spikes pollen samples were taken and the pollen used for crosses with an American tetraploid rye variety available. All the kernels harvested were sown and the chromosome numbers of the offspring determined. The behaviour of the different spikes was the following:

Spike No. 1. Two pollen samples from this spike gave an average diameter of the pollen grains of $39{,}52 \pm 0{,}39$ and $43{,}00 \pm 0{,}43$ units. A diploid plant of Östgöta Gråråg gave the corresponding value $33{,}24 \pm 0{,}31$. Four plants of diploid American rye had an average pollen diameter ranging from $33{,}32 \pm 0{,}39$ to $38{,}67 \pm \pm 0{,}45$. Four tetraploid plants belonging to the same variety had average values ranging from $38{,}30 \pm 0{,}57$ to $45{,}20 \pm 0{,}51$. Thus, it is clear that Spike No. 1 was tetraploid. This ear had been open-pollinated but did not produce a single seed.

Spike No. 2. The average pollen diameter was found to be $38{,}00 \pm 0{,}46$, thus strongly indicating that the spike was tetraploid. This was found to be true. After open pollination one single kernel was produced and this gave a triploid plant ($2n = 21$). The pollen from this spike was used for crosses with the tetraploid American variety. Two seeds were obtained, one of these did not germinate, but the other gave a tetraploid plant ($2n = 28$).

Spike No. 3. Two pollen samples measured indicated diploidy, the average values being $33{,}26 \pm 0{,}26$ and $32{,}31 \pm 0{,}31$. However, after pollination with the pollen of American tetraploid rye one seed was produced, and this gave a tetraploid plant ($2n = 28$). The reciprocal cross gave no seeds. These results indicate that the spike itself was a chimæra.

Spike No. 4. Fifteen seeds were harvested after open pollination. These seeds gave 13 plants, which were all found to be diploid ($2n = 14$).

Spike No. 5. Five seeds after open pollination gave 4 diploid plants ($2n = 14$).

From the above account it is evident that of the six tillers produced (including the one fixed) two were diploid, three tetraploid and one probably a diploid-tetraploid chimæra. The chimærical nature of the entire plant is thus quite clear. Morphologically, however, it was not possible with certainty to distinguish between diploid and tetraploid parts.

In the present connection the mode of meiosis in the tetraploid spike fixed is of particular interest. The following results were obtained.

As in most other autotetraploids *first metaphase* was characterized by the presence of a variable number of quadrivalents. In 24 completely analysed metaphase groups the number of quadrivalents was found to range from 0 to 6, the average number being 2,33. Figs. 120—121 show the two extreme configurations observed, viz. 14_{II} and $6_{IV} + + 2_{II}$. Besides quadrivalents the cells usually contained only bivalents, but in several cases also trivalents and univalents. More precisely, the configurations and frequencies observed were the following:

Configuration	No. of cells	Configuration	No. of cells
14_{II}	1	$1_{IV} + 1_{III} + 10_{II} + 1_{I}$	1
$1_{IV} + 12_{II}$	2	$1_{III} + 12_{II} + 1_{I}$	1
$2_{IV} + 10_{II}$	4	$1_{IV} + 11_{II} + 2_{I}$	1
$3_{IV} + 8_{II}$	3	$2_{IV} + 1_{III} + 8_{II} + 1_{I}$	4
$4_{IV} + 6_{II}$	2	$2_{IV} + 1_{III} + 6_{II} + 5_{I}$	1
$5_{IV} + 4_{II}$	1	$3_{IV} + 1_{III} + 6_{II} + 1_{I}$	2
$6_{IV} + 2_{II}$	1		

The average number of univalents in these cells is 0,63. The frequency of univalents was also studied in 100 not completely analysed metaphase groups. The following values were obtained:

	Number of univalents			
	0	1	2	3
Number of cells:	51	35	9	5

The average value is 0,68 which closely corresponds to the value 0,63 obtained from the 24 completely analysed I—M groups.

The quadrivalents were either rings or chains, and it is rather remarkable that no other configurations could be detected. This fact distinguishes the quadrivalents formed by four homologous chromosomes from the interchange quadrivalents of »Type *c*», described above.

A total of 56 quadrivalents were observed, and of these 37 were zig-zag-arranged (22 chains and 15 rings) and 19 (9 chains and 10 rings) non-zig-zag-arranged. No accurate counts of the chiasma frequency could be made, but it may be mentioned that of 203 bivalents observed in the 24 analysed cells of the tetraploid spike 148 were rings and 55 were rods. This gives the percentage values $72{,}9 \pm 3{,}1$ and $27{,}1 \pm 3{,}1$ respectively. The frequency of ring and rod bivalents was also counted in four diploid sister plants and in all of these the frequency of ring bivalents was higher than in the tetraploid, the percentage values being $86{,}6 \pm 1{,}6$, $79{,}8 \pm 2{,}8$, $93{,}3 \pm 2{,}3$ and $87{,}5 \pm 2{,}6$ respectively. As the chiasma number per chromosome in the quadrivalents is relatively low, and at any rate lower than in the ring bivalents, this must signify that in the tetraploid the average chiasma frequency per chromosome is lower than in the diploids. According to UPCOTT (1939) tetraploids have generally a lower chiasma frequency than the corresponding diploids.

At *first anaphase* (cf. Fig. 122) the regular distribution 14—14 was observed in 10 cells, 13—15 in 2 cells and 14—1—13 in one cell. Lagging and division of univalents at I—A were rare. In 50 cells observed the number of such bodies ranged from 0—2, the average value being 0,30. In a few cases difficulties of separation and other slight irregularities were observed, but in the main this stage was rather regular. At late anaphase and telophase, however, small chromatin-like dots were frequently observed in the plasm, but the true nature of these dots is not known.

Interphase was nearly always normal in appearance. A few cells studied showed the regular chromosome distribution 14—14. Eliminated bodies outside the interphase nuclei were quite rare.

At *second anaphase* one or a few lagging chromosomes were observed in about half of the cells. More precisely, the following frequencies were found in 112 cells studied:

Number of lagging chromosomes: ...	0,0	0,1	0,2	1,1	1,2	1,3	2,2
Number of cells:	59	14	2	25	5	1	6

The denomination 0,0 denotes no lagging in either of the two corresponding cells, 0,1 means a lagging chromosome in one of the cells but none in the other, etc.

The frequency observed was somewhat higher than expected, but on the whole it corresponds fairly well with the frequency of univalents dividing at I—A. As usual such split univalents will be distributed at random during the second division.

At II—A the lagging chromosomes often showed rather marked constrictions and, for instance, when there was one lagging chromosome in each of the two cells

of the same p. m. c., these corresponding laggards were usually found to have the same chromosome morphology. On the other hand, laggards in different p. m. c. sometimes represented different morphological types. These conditions are illustrated in Figs. 125 and 126.

One abnormality observed at this stage should be mentioned. In each of three neighbouring p. m. c. a dicentric chromatid was observed (Figs. 123—124). One of these (Fig. 123, indicated by an arrow) had evidently connected the two I—A groups and was now at II—A apparently broken by the cell wall. The other two dicentric chromatids, on the other hand, were stretched between the poles of the II—A groups in the same cell.

Since these three cells were situated close to each other they have probably originated from the same premeiotic cell. In this cell an inversion must have occurred, which gave rise to the dicentric chromatids after chiasma formation and crossing-over.

Finally, it remains to be said that the young tetrads in the tetraploid spike had a quite regular appearance and contained very few eliminated chromosomes outside the nuclei. One or two such bodies were observed in only 11 out of 74 complete tetrads studied.

8. THE FREQUENCY OF CHROMOSOMAL ABERRATIONS.

The frequency of the various cytological aberrants observed is given in Table 1. The first two series represent plants of the varieties »Stålråg» and »Östgöta Gråråg», taken completely at random from the populations. In the first variety 10 per cent of the plants showed quite obvious aberrations (in this case: segmental interchange). On the other hand, 65 per cent had quite regular meiosis. The remaining 25 per cent represent plants showing various slight irregularities, including inversions. In the other variety the corresponding figures were 4, 48 and 48 respectively. As there is no clear difference between the two series their values may be added. The total series has an average of 7 per cent obvious aberrations.

The third and fourth series of Table 1 represent a population material which was not taken entirely at random. The plants in question are the daughters of open-pollinated mother plants, but these mother individuals were selected plants, having a more or less poor seed-setting. This selection was made as it was assumed that plants with poor fertility should more frequently represent chromosomal aberrations than plants with good fertility. However, this selection of the mother plants does not seem to have increased the frequency of aberrations in the offspring, the average percentage of obvious aberrants being as low as 5.

Finally, Table 1 comprises two other series of offspring from open-pollinated but selected mother plants. Series No. 5 represents 22

TABLE 1. *Cytological aberrations in population plants of rye.*

Category	Meiosis quite regular	Various slight irregularities (including cytomixis)	Inversions	Segmental interchange	2n + 1 and 2n + 2f	Tetraploid — diploid chimæra	n	Per cent plants with quite regular meiosis	Per cent quite obvious aberrations [1]
»Stålråg», without selection	13	3	2	2	—	—	20	65	10
»Östgöta Gråråg», without selection	12	10	2	—	—	1	25	48	4
Total	25	13	4	2	—	1	45	56	7
»Stålråg», progenies from spikes with poor seed setting	4	3	—	—	2	—	9	44	22
»Östgöta Gråråg», progenies from spikes with poor seed setting	37	28	1	1 (?)	1	—	68	54	3
Total	41	31	1	1 (?)	3	—	77	53	5
»Stålråg», progenies from plants heterozygous for an inversion	16	6	—	—	—	—	22	73	0
»Stålråg», progenies from plants heterozygous for segmental interchange	16	4	—	3	—	—	23	70	13
The whole material	98	54	5	6	3	1	167	58,7	6,0

[1] The category »Quite obvious aberrations» includes the plants showing segmental interchange, extra chromosomes and a diploid-tetraploid chimærical constitution.

daughter plants of 2 mothers found to be heterozygous for small inversions, and Series No. 6 represents the progeny of a plant heterozygous for segmental interchange. The percentage of obvious aberrants in these progenies was found to be 0 and 13 respectively.

If the total material studied is combined into one series, this series will contain 6 per cent of plants with obvious meiotic aberrations. As is evident from series 1 and 2 this value represents rather well the average frequency in the populations studied. *Thus, on an average, every 15th or 20th plant in a field of the rye varieties »Stålråg» or »Östgöta Gråråg» is cytologically clearly aberrant and only slightly more than half of the plants have a perfectly regular meiosis.*

III. DISCUSSION.

Though the material studied was on an average more regular than expected, quite a number of different kinds of chromosomal aberrations were observed. Thus, heterozygosity for segmental interchange was found to occur in three unrelated population plants. Two of these individuals were characterized by an association of four chromosomes in almost all the pollen mother cells. The two plants, however, were found to represent different cases of segmental interchange, the quadrivalent associations showing characteristic peculiarities. Thus, »Type *c*» showed a higher percentage of chain quadrivalents than »Type *a*» and was further characterized by a conspicuous chromatin lump. This lump was situated between two special chromosomes and had in most cells exactly the same size and appearance. In a minority of the I—M groups it was replaced by another but equally characteristic structure (cf. Figs. 94—95, 98, 102, 104, 109—110). In the former case the lump probably contains one interstitial and one terminal chiasma, in the latter case the structure in question is probably formed by one interstitial chiasma only. At early diakinesis a special part of the quadrivalent was almost regularly found to be separated from the rest of the quadrivalent by a very marked constriction or rather by a thin thread (cf. Figs. 80—81, 83, 85—86 and 89). This special part probably corresponds to the characteristic lump seen at first metaphase. The true nature of all these structures is not yet clear, but it is probable that observations of similar structures in a certain line of inbred rye will give more complete information.

In the offspring of a segmental interchange plant representing »Type *a*» one plant (»Type *b*») was found to be characterized by the

regular occurrence of *two* quadrivalent associations. The plant in question had been raised after open pollination of the mother plant. Thus, the second quadrivalent (which was generally ring-shaped like the first one) must be due to the occurrence of another case of segmental interchange in the population.

Besides exchanges of relatively large segments some evidence was also obtained as to the occurrence of heterozygosity for exchange of small segments. Thus, in Type *c* a single cell showed $2_{IV} + 3_{II}$ instead of $1_{IV} + 5_{II}$. In another plant (»Type *d*») meiosis was on an average quite regular, but a single deviating I—M group clearly had $1_{III} + 1_{I} + + 5_{II}$ instead of 7_{II}. The rare occurrence of multivalents in these cases may be due either to the smallness of the segments exchanged or to the fact that the exchanges have just occurred in the plants and are only represented by single pollen mother cells or small local sectors. Such a sector was observed in rye by DARLINGTON (1933), who found a group of eight pollen mother cells with an interchange, all the other p. m. c. being normal.

In the offspring of a plant heterozygous for segmental interchange 50 per cent of the individuals should be heterozygous for the interchange and show an association of four chromosomes at meiosis. This should occur after selfing as well as after open pollination. — Meiosis was studied in 30 daughter plants of the plant *R. 525*, belonging to »Type *a*». Twenty-one of these plants had been raised after open pollination and 9 plants after isolation. In the former group not less than 19 plants had regular meiosis with 7_{II}, one plant had one quadrivalent and another plant (Type *b*) had two quadrivalents. Among the 9 plants after isolation 6 were normal, having 7_{II}, and the remaining three had $1_{IV} + 5_{II}$. Thus, in both categories, and especially in the first one, there is a pronounced deficiency of plants heterozygous for the interchange. The ratio 19 : 2 cannot represent a 1 : 1 ratio (D/m = 3,68) and neither 25 : 5 (D/m = 3,72), which ratio represents the entire material. Thus, the gametes carrying the interchange seem to be less successful than those representing the normal condition. Whether this is due to the interchange as such or to deleterious mutations accompanying the interchange (as has been inferred for *Drosophila*; cf. MULLER, 1930) cannot be decided. However, the important point is that *this case definitely demonstrates the occurrence of selective processes in a rye population.* Most probably it is a question of pollen tube competition, the occurrence of which was postulated in a previous paper (MÜNTZING, 1938, pp. 179—183).

Plants with 16 instead of 14 chromosomes have been observed by various workers especially in Japanese and Russian rye populations (cf. FERRAND, 1923; KIHARA, 1924; GOTHO, 1924; BELLING, 1925; STOLZE, 1925; EMME, 1927, 1928; LEVITSKY, 1931; LEVITSKY, MELNIKOV and TITOVA, 1932; DARLINGTON, 1933; HASEGAWA, 1934; LAMM, 1936; POPOFF, 1939 and FETISSOV, 1939). The finding of one plant of this kind in our material extends the occurrence of rye with 16 chromosomes to Swedish populations. In a progeny of this plant, raised after open pollination, several plants with 16 chromosomes could be selected. These plants were intercrossed last summer (1940) and in this way strains with 16 chromosomes may be raised. The detailed properties of these strains may be reported on another occasion. It may be mentioned already now, however, that in the offspring not only plants with 16 chromosomes were obtained but also many plants with other numbers, ranging from 14—20.

A comparison betweeen the meiotic behaviour of the mother plant and of other rye plants with $2n = 16$, described by previous workers, reveals that our plant is characterized by an unusually high degree of non-conjunction of the extra chromosomes, 8_{II} occurring in only 19 per cent of the pollen mother cells. This high degree of non-conjunction is certainly correlated with the rather small size of the extra chromosomes. In HASEGAWA's material, on the other hand (HASEGAWA, 1934), the 16 chromosomes regularly pair as 8_{II}, and the extra chromosomes are evidently larger than in our plants. Thus, rye with 16 chromosomes does not always mean the same thing. This was clear already from DARLINGTON's observations (1933) of a plant with two extra non-pairing fragments of different sizes.

A plant with $2n = 16$ studied by FETISSOV (1939) is exceptional in having a high degree of non-conjunction of *all* chromosomes and frequent irregularities correlated with this bad pairing. It is doubtful whether these irregularities are really caused by the extra chromosomes, as, according to our observations, varying degrees of non-conjunction may also occur in population plants without extra chromosomes. *A priori* it might be assumed, however, that the presence of extra chromosomes should have a tendency to upset the normal course of meiosis. In our 16-chromosome plant some anthers and loculi showed »cytomixis» resulting from premeiotic irregularities. On the other hand, a still more extreme case of cytomixis was observed in a population plant without extra chromosomes.

In the two trisomic individuals occurring in our material the extra

chromosome seemed to be of the same size as the homologous chromosomes. However, in the majority of the p. m. c. the extra chromosome occurred as a univalent, the frequency of trivalents being $40{,}80 \pm \pm 5{,}83$ at diakinesis and $29{,}40 \pm 6{,}38$ at first metaphase. In a trisomic rye plant described by TAKAGI (1935) the extra chromosome was paired more frequently, the percentage of trivalents at I—M being $47{,}20 \pm 3{,}16$. As in TAKAGI's case, too, the satellite chromosome seems to be involved, it is of interest to compare the frequencies. The difference $47{,}20 - 29{,}40$ is $17{,}80 \pm 7{,}12$ and since D/m will be 2,50 this difference is rather significant. This may be due either to different environmental or genetical conditions or to a size difference between the satellite chromosomes in TAKAGI's and our material.

Tetraploid-diploid chimæras have been observed in several plant species. The occurrence of such a plant in an ordinary rye field is especially interesting from the point of view that such a plant will be a source of further cytological aberrations. As mentioned above, one of the tetraploid spikes produced a single seed after open pollination, and this seed gave a triploid plant. This plant unfortunately died, but from work with other tetraploid strains of rye it is known that vigorous triploid hybrids can be obtained from crosses between tetraploids and diploids. Such triploids have relatively good fertility, and when pollinated with pollen from diploids give a progeny with chromosome numbers ranging from 14 to 21. Most of these plants have 14—16 chromosomes, the trisomics with 15 chromosomes being especially frequent (MÜNTZING, unpublished results). Thus, the occasional occurrence of tetraploid plants or spikes in a rye population may give rise to swarms of new cytological aberrations. As, for instance, triploids and trisomics are also known to give rise to structural chromosome changes, the aberrations will not be numerical only.

Finally, the occurrence of inversions should be considered. In all the plants found to be heterozygous for inversions the segments inverted must have been rather small, judging from the low frequency of dicentric chromatids and fragments at I—A. Chromatin bridges of this kind seem to be frequent in inbred lines of rye (LAMM, 1936, and unpublished results of the present writers). This is surprising in a material that should be homozygous and indicates the possibility that in the inbred lines as well as in the populations it may be a question of inverted duplications rather than simple inversions.

From the above report it is clear that several different kinds of chromosomal aberrations occur in ordinary rye populations. It is

difficult to state the exact frequency of aberrant plants in our material, the transitions between regular meiosis and marked irregularities being rather continuous. However, the values given in Table 1 probably reflect the true situation rather well.

The average value of 6 per cent obvious aberrants in our material may seem to be rather high, but in the Bulgarian rye populations studied by POPOFF (1939) the frequency was evidently still higher. This material was very polymorphic and contained a high proportion of more or less sterile plants. The somatic chromosome numbers were determined in the offspring of fertile as well as partially sterile individuals. In the latter progenies in particular numerous aberrants with 1—4 extra chromosomes were observed, plants with 16 instead of 14 chromosomes being especially frequent. POPOFF suggests that the occurrence of these aberrations is due to crosses between ordinary rye and the wild rye, *Secale montanum*. This may be true of the Bulgarian material, which is not so far removed from the centre of origin of cultivated rye. However, since *Secale montanum* does not occur in Sweden such an explanation is not possible for our own material, which also included a low proportion of numerical aberrants. As pointed out above, rye plants with 15 and 16 chromosomes or even more aberrant numbers may arise in the offspring of spontaneous tetraploids, triploids or trisomics. The trisomics may either arise in the progeny of triploids or are the result of non-conjunction, a phenomenon frequently observed in the population plants.

In his paper POPOFF only mentions the occurrence of numerical aberrants with extra chromosomes. It is highly probable, however, that more extensive meiotic studies of this interesting material will reveal the presence of segmental interchange and other structural aberrations, as in our case. From POPOFF's values and descriptions it is rather clear that his material is still more irregular as regards fertility and meiotic behaviour than the Swedish populations studied by us. This difference is probably caused by the fact that the Swedish populations have been subjected to a more intensive selection than the more primitive varieties studied by POPOFF.

At any rate, the population studies undertaken by POPOFF and ourselves, in combination with the numerous scattered observations by previous workers of rye plants with aberrant chromosome numbers, clearly demonstrate that *the species Secale cereale is not cytologically stable*. Most rye plants, it is true, have a regular or almost regular meiosis, but in addition to these there is a considerable proportion of

numerical or structural aberrants, which can easily be found in any rye field.

Now since rye is characterized by a rather frequent occurrence of partial sterility as well as cytological aberrations it lies close at hand to assume a causal connection between the two phenomena. Indeed, in POPOFF's material (POPOFF, 1939) the degree of partial sterility was found to be proportional to the number of extra chromosomes present. — The fertility conditions and the correlation between fertility and meiotic behaviour in our material may be considered in detail in a later paper. However, already now it can be stated that sterility in rye is not only haplontic and caused by the formation of special inviable classes of gametes. An important part of the rye sterility is also diplontic, i. e. caused by disturbances in the diplophase. This is evident from the following facts:

1. There is often a good deal of fertility variation in different parts of the same plant.

2. Cytological irregularities, for instance, cytomixis, may be more pronounced in some flowers, anthers or loculi than in others.

3. The variety »Östgöta Gråråg» is on an average more sterile than the variety »Stålråg», but this difference is not correlated with a higher frequency of chromosomal aberrations in the former variety (cf. Table 1).

4. Triploid rye plants have surprisingly good pollen. Since most of the pollen grains will receive unbalanced chromosome complements, a considerable and visible degree of sterility should be expected, if the partial sterility in ordinary population plants is haplontic and due to structural or numerical disturbances. — It is possible, however, that intrachromosomal structural disturbances may have a more drastic effect than an interchromosomal lack of balance.

Even if the sterility in rye populations should turn out to be diplontic to a rather high extent, this does not exclude a causal connection between sterility and chromosomal disturbances. As a working hypothesis the following situation may be suggested:

The idea of a normal standard set of chromosomes in rye (and other allogamic organisms) may imply a rather rough schematizing. More probably there is no definite standard type of chromosome structure and definite deviations from this type. On the contrary, the chromosome complements received by the gametes after meiosis are probably rather frequently different in several structural details. Sometimes the differences carried by the two gametes forming a new in-

dividual are great enough to give rise to multiple associations or other conspicuous deviations. In most cases, however, the differences are too slight to influence the chromosome pairing observed from diplotene to first metaphase.

If really the chromosome complements differ in this way, containing chromosomes that are incompletely homologous, this should also influence the diplophase. Then it will often happen that the rye plants are quantitatively disturbed with respect to chromatin balance, i. e. they will represent more or less pronounced deficiencies and duplications. This will certainly influence vitality as well as fertility. Disturbances of this kind as well as the formation of special, lethal categories of gametes must lead to sterility, and partial sterility is, indeed, a phenomenon which seems to characterize allogamous in contrast to autogamous diploid plant species (MÜNTZING, 1938, 1939). Thus, the theory is supported in part by the actual occurrence of this sterility but also by the demonstration of chromosomal aberrations in the populations of rye. Evidence of a similar kind from other species has already been discussed by MÜNTZING (1938 and 1939).

We admit that so far the argumentation is rather hypothetical, and at present the main thing is to gather more data. Besides giving an account of the fertility conditions in our material and the inheritance of different degrees of fertility, the next steps of the investigation, which are now being carried out, will be a study of meiosis in relation to fertility and vitality in inbred lines of rye and in F_1 hybrids between such lines. At the same time the probable occurrence of structural chromosome differences between the lines will be looked for, especially with the aid of the promising fixation methods used by SHMARGON (1938) and other Russian workers. In an inbred line of rye KATTERMANN (1939) has already observed a new characteristic chromosome type, occurring in homo- or heterozygous condition.

By means of work of the kind outlined above it may be possible to obtain some further evidence as to the constitution of rye and of allogamous species in general. At the same time it may perhaps be possible to elucidate the inbreeding phenomena to a certain extent. Though the possibility of plasmatic causes of inbreeding degeneration should not be overlooked (cf. HERIBERT NILSSON, 1937; WINGE and LAUSTSEN, 1940), it seems rather probable that the sterility in the populations and at least part of the degeneration in the inbred lines may have the same basic cause, viz. the supposed, and now partly

demonstrated, structural polymorphism. In the populations the gametes will supplement each other, in the inbred lines the more or less dangerous consequences of a onesided chromosomal constitution will be apparent.

IV. SUMMARY.

1. Meiosis was studied in population plants of rye, belonging to the Swedish varieties »Stålråg» and »Östgöta Gråråg». Of 167 plants examined 98 had a quite regular meiosis with 7_{II}, 53 plants showed minor irregularities such as non-conjunction, difficulties of separation and fragmentation at I—A, etc. Five plants were heterozygous for small inversions and 6 plants for segmental interchange. Two individuals were trisomic for the satellite chromosome, one plant had an extra pair of generally unpaired small chromosomes, and one plant was a diploid-tetraploid chimæra. Cytomixis due to premeiotic irregularities was observed in two plants. A more or less detailed account of meiosis in the various aberrant types is given.

2. The plants heterozygous for segmental interchange belonged to several different categories, which could be distinguished by different types and frequencies of multiple associations. One plant had regularly $2_{IV} + 3_{II}$. In the offspring of an individual with $1_{IV} + 5_{II}$ there was a significant excess of plants with 7_{II}. This must be due to pollen tube competition or some other selective process.

3. The observed occurrence of tetraploidy in a rye population will lead to the production of triploids and in later generations to various numerical and probably also structural aberrants. The average frequency of quadrivalents in the tetraploid spike studied was 2,33, and the average chiasma frequency per chromosome was found to be lower than in diploid sister plants.

4. The present investigation, in combination with the results of previous workers, demonstrates that the species *Secale cereale* is not cytologically stable. This lack of stability is correlated with a frequent occurrence of partial sterility. The nature and causes of this sterility and its probable connection with the inbreeding phenomena are discussed.

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Corrigenda. — In Fig. 121 (p. 292) the white spot on the 2nd quadrivalent from the right should be removed. In Fig. 122 there is in reality a faint chromatin bridge just below the fragment, connecting the two anaphase groups.

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EINE SEGREGATE FORM VON SALIX CAPREA, DIE DURCH STECKLINGE VERMEHRT WERDEN KANN

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UNTER den Nachkommen der F_2 des Bastards *Salix viminalis* × *caprea*, über die ich früher ausführlich berichtet habe (HERIBERT NILSSON, 1918), fand ich auch einen Strauch, der in allen Eigenschaften, vegetativ und floral, ganz mit *S. caprea* übereinstimmte (l. c. S. 47 und 68, Fig. 30). Da sich *S. caprea* von allen schwedischen und übrigen mir bekannten Weidenarten dadurch unterscheidet, dass sie keine Adventivwurzeln zu treiben vermag, also nicht durch Stecklinge vermehrt werden kann, war es von besonderem Interesse zu untersuchen, ob auch der erwähnten Form, die ich f. *capreosegregata* nenne, diese Eigenschaft zukommt. Mehrere Versuche, sie in anderen Gärten in dieser Weise einzupflanzen, misslangen vollständig, und auch weitere methodische Versuche mit Stecklingvermehrung hatten keinen Erfolg. Die f. *capreosegregata* schien also auch in dieser Eigenschaft eine reine *caprea* zu sein.

Später (1930) habe ich indessen eine Kreuzung zwischen dieser Form und ihrem ♂-Elter ausgeführt, weil ich sehen wollte, ob die Nachkommenschaft habituell mit einer *caprea*-Population übereinstimmte. Dies traf zu. Kein einziger Strauch verriet einen Einschlag von *viminalis*. Die f. *capreosegregata* war also eine ganz rekurrente Kombination, die in der Elternpopulation weder selbst noch in bezug auf die Nachkommenschaft morphologisch konstatiert werden konnte. Dass die Kreuzung *capreosegregata* × *caprea* betreffs der Adventivwurzelbildung spalten könnte, fiel mir nicht ein, da beide mit Stecklinge nicht vermehrt werden konnten.

Eine unvermeidliche Umpflanzung eines grossen Teils meines *Salix*-Materials von Alnarp, wo ich von 1928—1932 meine Versuche hatte, nach Källby bei Lund, wo ich endlich mein fünftes und definitives Salicetum erhalten habe, brachte indessen das Gute mit sich, dass auch die betreffende Kreuzung in bezug auf Stecklingvermehrung geprüft wurde. Ich war vom Misslingen dieser Vermehrung so über-

zeugt, dass ich die Nachkommensteckinge — da ich im Bestand keine Lücken haben wollte — nicht in Källby sondern im Botanischen Garten zu Lund pflanzte, wo ich sie unter dem Material, das für gelegentliche Vermehrung bestimmt war, aussetzte.

Zu meinem grossen Erstaunen zeigten mehrere der Nachkommen

Fig. 1. Rechts Steckling des *caprea*-Elters, der unten aus dem grossen Kallus keine Wurzeln treibt, aber im ganzen Unterwasserteil auffallende aërenchymatische Protuberanzen aufweist; links Steckling eines Individuums aus der Kreuzung f. *capreosegregata* × *caprea* mit reicher Wurzelbildung.

eine ganz gute Entwicklung. Sie schossten schnell und kräftig, so gut oder fast so gut wie *viminalis*. Andere aber verhielten sich wie *caprea*; kein einziger Steckling von diesen trieb seine Knospen aus, sondern die Zweigstücke verdorrten während des Sommers. Offenbar spaltete die Nachkommenschaft von *capreosegregata* × *caprea*. Das Verhältnis zwischen den wurzeltreibenden und nicht wurzelbildenden Sträuchern war 15 : 9.

Der grosse Unterschied in bezug auf das Vermögen, Adventivwurzeln bei Wasserkultur zu bilden, zeigt Fig. 1. Der Steckling rechts stammt von *S. caprea*, dem ♂-Elter des Bastards. An der Basis des Stecklings hat sich ein grosses Kallusgewebe gebildet, aber es zeigt sich keine Tendenz zu Wurzelbildung. Dagegen sind die aërenchymatischen Protuberanzen, die sich an *Salix*zweigen bei Wasserkultur aus den Lentizellen leicht bilden, ungewöhnlich stark entwickelt. Der Steckling links in Fig. 1 gehört einem Strauch (Nr. 3582) der Kreuzung *capreosegregata* × *caprea* an. Am basalen Kallus treten hier mehrere und gut entwickelte Wurzeln auf. Die Lentizellenwucherungen sind dagegen nur als unbedeutende Intumeszenzen entwickelt.

Die vorliegenden Versuche zeigen, dass eine alternative und distinkte Spaltung in bezug auf die Fähigkeit der Adventivwurzelbildung bei den Arten *S. caprea* und *viminalis* stattfindet. Wie aber diese faktoriell zu deuten ist, kann aus dem bisher vorliegenden, geringen Material nicht ermittelt werden. In F_1 der Kreuzung *viminalis* × *caprea* hatte ich 26 Sträucher (HERIBERT NILSSON, 1918, p. 10). Von diesen sind nur die Ausgangspflanzen für F_2 bei der Umpflanzung nach Alnarp und Lund durch Stecklinge untersucht worden. Beide zeigten gute Adventivbewurzelung. Der *capreosegregata*-Strauch ist also aus Eltern hervorgegangen, die stecklingvermehrt werden können, hat aber selbst nicht diese Fähigkeit. Er muss wohl als rezessiv ausgelesen betrachtet werden. *S. caprea* kann aber nicht als rezessiv angesehen werden, denn *capreosegregata* × *caprea* restituiert Adventivwurzelbildung, muss also wohl »hemmende» Faktoren besitzen. Aber *viminalis* dominiert! Wie nun diese Tatsachen vereint werden können, darüber können nur weitere Versuche entscheiden. Ich habe indessen schon jetzt über das erhaltene Resultat berichten wollen, da es vom theoretischen Gesichtspunkte von nicht geringem Interesse ist. Denn es zeigt, dass aus einer Kreuzung zwischen Arten, die sich in der Natur wohl kreuzen, aber nie vermischen, extreme rekurrente Individuen auftreten können, die *morphologisch* ganz einer der Arten angehören und *taxonomisch* nicht klargelegt werden können. Durch diese wird aber die Variabilität der Art vergrössert, und plötzlich kann man eine Eigenschaft finden, die ganz für eine andere Spezies charakteristisch ist, ohne dass man diagnostisch in bezug auf andere Eigenschaften einen »Einschlag» dieser Spezies feststellen kann. Der mitgeteilte Versuch bildet hierfür ein Paradebeispiel. Denn *capreosegregata* musste offenbar auch in der Natur in *S. caprea* resorbiert werden und eine ganz lokale Variabilität betreffs des Vermehrungsvermögens durch

Stecklinge verursacht haben. Die Art wäre dann auch sogleich praktisch wertvoller geworden, weil gewisse Sträucher nunmehr durch Stecklinge wie die übrigen Weiden vermehrt werden könnten. In meinem Versuch ist dieses praktische Problem jedenfalls schon gelöst.

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VERERBUNGSSTUDIEN AN DER SCHMETTERLINGSART LEUCODONTA BICOLORIA

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DIE Schmetterlingsart *Leucodonta bicoloria* SCHIFF. tritt in zwei, in bezug auf ihre Färbung voneinander erheblich abweichende Formen auf. Die Grundfarbe der Flügel ist bei beiden schneeweiss. Die Hauptform (f. *typica*; Fig. 1 *a* und *b*) hat auf den Vorderflügeln eine aus schwarzen Flecken bestehende innere Querlinie und eine äussere solche, die ebenso durch schwarze Pünktchen angedeutet ist. Nach aussen ist die innere Querlinie von orangegelben Flecken eingefasst; am Hinterrand des Flügels reicht die orangegelbe Farbe bis an die äussere Querlinie heran und jenseits derselben befindet sich noch ein weiterer Fleck gleicher Farbe. Die Männchen haben im allgemeinen mehr Pigment als die Weibchen. Der aberrativen Form (Fig. 1 *c* und *d*) fehlen die orangegelben Zeichnungen hingegen völlig. Einige Individuen (ab. *albida* BOISD.; Fig. 1 *c*) zeigen am Vorderflügel geringfügige schwarze Fleckchen, anderen wiederum fehlt jede Zeichnung und die Tiere sind einfarbig schneeweiss (ab. *unicolora* MÉN.; Fig. 1 *d*). Die beiden Aberrationen sind durch Übergänge miteinander verbunden. — Zu bemerken ist, dass die letztgenannten Formen ein anderes Verbreitungsgebiet als die Hauptform haben (vgl. unten).

In den nachstehend geschilderten Kreuzungsversuchen wurden die Vererbungsverhältnisse der Flügelfärbung der genannten Art untersucht. Der Einfachheit halber werden die Hauptform hier als »orangegelb», die ab. *albida* und ab. *unicolora* gemeinsam als »weiss» bezeichnet.

Die Kreuzungsversuche. — Sämtliche Versuchstiere stammen von einem, in der Gegend von Porvoo in Südfinnland erbeuteten Weibchen. Dieses war orangegelb; das Männchen und der Vater der Zucht ist unbekannt. Von der Nachkommenschaft dieses Weibchens entwickelten sich 17 zu Imagines; 11 waren orangegelb und 6 weiss. Mit diesem Material wurden folgende vier Kreuzungen ausgeführt. (Da die Vererbung der Farben bei beiden Geschlechtern dieselbe ist, wird von einer gesonderten Angabe der Geschlechter abgesehen.)

Kreuzung	*1.*	♀ orangegelb × ♂ weiss:	11	orangegelb;	14	weiss
»	*2.*	♀ » × ♂ » :	1	»	3	»
»	*3.*	♀ weiss × ♂ orangegelb:	6	»	8	»
»	*4.*	♀ orangegelb × ♂ orangegelb:	33	»	10	»

Mit den aus diesen Kreuzungen hervorgegangenen Individuen wurden weiter folgende 12 Kreuzungen ausgeführt. (Die nach den Zeichen ♀ und ♂ in Klammern stehenden Ziffern beziehen sich auf die Ordnungszahl der obigen Kreuzungen.)

Kreuzung	*5.*	♀ (*4*) orangegelb × ♂ (*3*) weiss:	13	orangegelb;	11	weiss
»	*6.*	♀ (*1*) » × ♂ (*1*) » :	1	»	3	»
»	*7.*	♀ (*4*) » × ♂ (*1*) » :	32	»	29	»
»	*8.*	♀ (*1*) weiss × ♂ (*4*) orangegelb:	22	»	17	»
»	*9.*	♀ (*4*) » × ♂ (*4*) » :	8	»	9	»
»	*10.*	♀ (*2*) » × ♂ (*3*) » :	8	»	11	»
			Insges.:	84	orangegelb;	80	weiss

Kreuzung	*11.*	♀ (*3*) weiss × ♂ (*1*) weiss:		13	weiss
»	*12.*	♀ (*3*) » × ♂ (*2*) » :		7	»
»	*13.*	♀ (*1*) » × ♂ (*1*) » :		6	»
		Insges.:		26	weiss

Kreuzung	*14.*	♀ (*4*) orangeg. × ♂ (*1*) orangeg.:	44	orangegelb;	13	weiss
»	*15.*	♀ (*4*) weiss × ♂ (*4*) orangegelb:	7	orangegelb		
»	*16.*	♀ (*4*) orangeg. × ♂ (*3*) orangeg.:	11	orangegelb		

Die Versuchsergebnisse. — Die obigen Kreuzungsresultate zeigen, dass wir es hier mit einer monohybriden Mendelspaltung zu tun haben. Die Färbung der Hauptform (orangegelbe Flecken nebst deutlichen schwarzen Zeichnungen) ist dominant. Die zur Hauptform gehörigen Individuen können daher entweder homozygot (*AA*) oder heterozygot (*Aa*) sein. Die einheitlich weisse Färbung oder die mit spärlicher schwarzer Zeichnung ist wiederum rezessiv. Sämtliche weissen Individuen sind somit homozygot (*aa*).

Das in der Natur erbeutete Weibchen, von dem sämtliche Versuchstiere abstammen, war heterozygot orangegelb (*Aa*). Auf Grund der Nachkommenschaft zu schliessen ist es von einem weissen Männchen (*aa*) befruchtet worden, was umso wahrscheinlicher erscheint, als in Finnland die weisse Form ausgesprochen überwiegt. Es handelt sich also um eine gewöhnliche Rückkreuzung, die zur Hälfte orangegelbe

(*Aa*) und weisse (*aa*) Nachkommen liefert. Das Resultat 11 : 6 weicht zwar erheblich vom theoretischen Verhältnis ab, dürfte aber in den kleinen Zahlen begründet sein.

In den Kreuzungen *1—3* ist ebenfalls ein heterozygotes orangegelbes Individuum (*Aa*) mit einem weissen (*aa*) zusammengeführt worden, weshalb sich die Nachkommen auch hier zur Hälfte auf die beiden Gruppen verteilen müssten. Die Resultate entsprechen auch in grossen Zügen den Erwartungen. Kreuzung *4* bezieht sich wiederum auf zwei heterozygote orangegelbe Individuen (*Aa*), das Ergebnis müsste also $^3/_4$ orangegelbe (*AA* und *Aa*) und $^1/_4$ weisse Falter (*aa*) sein. In der Tat kommen die erhaltenen Zahlen den idealen sehr nahe.

Die Resultate der Kreuzungen *5—16* stehen gleichfalls mit den obigen durchaus im Einklang. In den Kreuzungen *5—10* handelt es

a *b* *c* *d*

Fig. 1. *Leucodonta bicoloria*. — *a*: f. *typica*; Männchen. — *b*: f. *typica*; Weibchen. — *c*: ab. *albida*; Männchen. — *d*: ab. *unicolora*; Weibchen. (Ung. $^4/_5$ nat. Gr.)

sich durchweg um solche zwischen einem heterozygoten orangegelben *Aa*-Individuum und einem weissen *aa*-Individuum. Der Erwartung gemäss verteilt sich die Nachkommenschaft etwa zur Hälfte auf die beiden Gruppen. In den Kreuzungen *11—13* sind beide Partner weiss, also homozygot rezessiv (*aa*); die Nachkommenschaft sollte demnach durchweg weiss ausfallen, was auch der Fall war. In Kreuzung *14* wurden zwei heterozygote orangegelbe Individuen (*Aa*) zusammengeführt. Wie ersichtlich, wurde recht nahe das theoretisch erwartete Verhältnis 3 : 1 gefunden. In Kreuzung *15* wurde ein homozygotes orangegelbes Individuum (*AA*) — von den orangegelben Individuen der Kreuzung *4* waren ja $^1/_3$ homozygot — mit einem weissen (*aa*) gekreuzt; sämtliche Nachkommen waren erwartungsgemäss orangegelb (*Aa*). An der Kreuzung *16* beteiligten sich ein homozygotes orangegelbes Weibchen (*AA*) und ein heterozygotes orangegelbes Männchen (*Aa*), was ausschliesslich orangegelbe Individuen geben sollte. Dies ist auch tatsächlich der Fall gewesen.

Wie bereits oben erwähnt, schwankt die schwarze Zeichnung auch bei den weissen Formen erheblich. Fig. 1 *c* und 1 *d* stellen Extremfälle dar, zwischen denen alle denkbaren Übergangsformen bestehen. Im allgemeinen sind die Männchen reicher gezeichnet; sämtliche vollweissen Individuen meiner Versuche waren Weibchen. Auf Grund der Versuche ist nicht zu entscheiden, ob das verschiedene Vorkommen von Pigment bei den weissen Individuen auf phänotypische Variabilität oder etwa auf polymere Faktoren zurückzuführen ist.

Frühere Versuche mit Leucodonta bicoloria. — FEDERLEY (1920, S. 243—245, 249—250) ist bei seinen Versuchen mit *Leucodonta bicoloria* bezüglich der Vererbung der Farben zu anderen Ergebnissen gekommen. Er ist der Ansicht, dass seine Versuche für das Vorkommen von polymeren Faktoren sprechen.

FEDERLEYS Material stammte aus Jaakkima am See Laatokka, wo die Art häufig im Mai und Juni flog. Da von den zahlreichen Individuen sämtliche den Formen *albida* und *unicolora* angehörten, glaubt FEDERLEY »versichern zu können, dass die Hauptform zu dieser Zeit in der betreffenden Gegend überhaupt nicht vorkam». Zwei in der Natur erbeutete *unicolora*-Weibchen, »die wohl mit allergrösster Wahrscheinlichkeit von *albida*-♂♂ befruchtet worden waren», legten Eier ab und aus diesen entwickelten sich alle drei Formen nebeneinander, und dazu noch alle Übergänge von *bicoloria* über *albida* bis *unicolora*. Die Exemplare verteilten sich folgenderweise auf die verschiedenen Formen: 8 *unicolora*, 4 *albida—unicolora*, 6 *albida*, 6 *albida—bicoloria* und 8 *bicoloria*. Da alle in der Natur gefangenen und beobachteten Falter den Formen *albida* und *unicolora* angehörten, unter ihren in der Gefangenschaft aufgezogenen Nachkommen aber trotzdem nicht weniger als 8 Exemplare auftraten, die der Hauptform sehr nahe kamen, findet FEDERLEY das Vorkommen von polymeren Faktoren sehr wahrscheinlich. Er hält es für möglich (S. 249), »dass die Form *unicolora* durch den Verlust von ein paar polymeren Faktoren entstanden ist, und die Form *albida* in bezug auf diese Faktoren heterozygotisch ist». »In diesem Fall müsste eine Kreuzung *albida* × *albida* alle möglichen Zwischenstufen von *bicoloria* bis *unicolora* ergeben. In unserem Fall handelte es sich vermutlich um eine Kreuzung *unicolora* × *albida*, weshalb man in der Nachkommenschaft eine überwiegende Anzahl *albida* und einige *unicolora* erwartet hätte. Da nun ausserdem noch Biotypen, die der Hauptform *bicoloria* nahe kamen, auftraten, so müssen wir voraussetzen, dass *unicolora* noch Faktoren besitzt, die mit anderen zusammen schwarzes und gelbes Pigment hervorrufen können.

Hier kann nur eine planmässig ausgeführte Vererbungsanalyse die exakte Antwort geben.»

Da in den oben referierten Versuchen FEDERLEYs das Männchen unbekannt ist, besteht natürlich die Möglichkeit, dass in einem der beiden Fälle das *unicolora*-Weibchen dennoch von einem heterozygoten Männchen der Hauptform befruchtet worden ist. Dann müsste von der Nachkommenschaft die Hälfte der Hauptform angehören. Andererseits ist indessen zu bemerken, dass die Versuche FEDERLEYs auch Übergänge zwischen der Hauptform und den weissen Formen gaben, während solche in meinen Versuchen überhaupt nicht vorkamen. Dies deutet auf die Möglichkeit hin, dass die *Leucodonta*-Formen FEDERLEYs von den phänotypisch ähnlichen Formen meiner Versuche genotypisch verschieden waren. Eine sichere Entscheidung der Frage ist unmöglich, da wir die Beschaffenheit der Männchen im ersteren Fall nicht mit Sicherheit kennen.

Besprechung der Ergebnisse. — *Leucodonta bicoloria* ist über den grössten Teil Mittel- und Osteuropas bis zum Ural verbreitet. Die Nordgrenze der Art erstreckt sich über Südwestengland, Südskandinavien und Mittelfinnland. Ausserdem kommt die Art in Ostasien vor. Zu bemerken ist, dass die verschiedenen Formen eine verschiedene Verbreitung besitzen. In West- und Mitteleuropa sowie in Skandinavien ist nur die Hauptform bekannt; diese ist überdies im gesamten übrigen Verbreitungsgebiet der Art (z. B. in Finnland, im Baltikum, in Russland und auch in Ostasien) zu finden. Die weisse Form (ab. *albida* und ab. *unicolora*) zeigt dagegen eine östliche Verbreitung, indem die westlichsten Fundorte in Finnland, in den baltischen Ländern und in Ostdeutschland (z. B. bei Kolberg) liegen. Die weissen Individuen sind im Bereich ihres Verbreitungsgebietes vielerorts (wenigstens in Finnland und Ostasien) der Hauptform bedeutend überlegen und in den betreffenden Gegenden offenbar vorherrschend.

Aus Obigem dürfte hervorgehen, dass bei *Leucodonta* die rezessive (weisse) Form die dominante (Hauptform) vielerorts an Häufigkeit übertrifft. (Es leuchtet ein, dass die weissen Formen nicht überall genotypisch identisch zu sein brauchen.) Unter den Schmetterlingen begegnen wir auch anderen deutlichen Fällen genannter Art. So ist die Weibchenform *valesina* von *Argynnis paphia* mancherorts (z. B. in Finnland) sehr selten, trotzdem sie dominant ist (Näheres bei GOLDSCHMIDT und FISCHER, 1922). Über weitere entsprechende Fälle siehe DOBZHANSKY (1937) und TIMOFÉEFF-RESSOVSKY (1939). Da die weisse Form von *Leucodonta* eine »einfache Mendelrasse» darstellt, ist es

offenbar, dass sie durch eine in der Natur stattgefundene Genmutation entstanden ist. Ausser dem sichtbaren morphologischen Unterschied in der Flügelfärbung muss die Mutation bei den fraglichen Schmetterlingen auch physiologische Veränderungen verursacht haben, denen zufolge die neue weisse Form dort lebenskräftiger ist, wo sie die dominante Hauptform an Häufigkeit übertrifft. Offenbar machen diese physiologischen Veränderungen es der neuen Form möglich, gewisse äussere Verhältnisse besser zu vertragen. Ohne experimentelle Untersuchungen ist es natürlich unmöglich zu sagen, um welcherlei physiologische Veränderungen und äussere Verhältnisse es sich hier möglicherweise handelt. Ich möchte indessen auf die grosse Übereinstimmung hinweisen, die zwischen der westlichen Verbreitungsgrenze der weissen Form von *Leucodonta* und derjenigen der »östlichen Temperaturrasse» von *Drosophila funebris* (TIMOFÉEFF-RESSOVSKY, 1939, S. 184—187; vgl. insbesondere Fig. 23) besteht. TIMOFÉEFF-RESSOVSKY (l. c.) hat experimentell nachgewiesen, dass die besagte Rasse von *Drosophila funebris* erhöhte relative Vitalität sowohl bei tiefer als auch bei hoher Temperatur zeigt. Da sie somit grössere Temperaturschwankungen besser verträgt, kann sie ein kontinentaleres Klima leichter als die westeuropäischen Rassen vertragen. Möglicherweise haben wir es auch bei *Leucodonta* mit etwas Ähnlichem zu tun. Auf jeden Fall ist die neue Form von *Leucodonta* unter bestimmten Verhältnissen lebenstüchtiger als die Stammform. Dies bildet also einen neuen Beweis dafür, dass eine Genmutation im Kampf ums Dasein besser ausgerüstet sein kann als ihre Stammform und somit in der Evolution einen Fortschritt bedeutet.

Dem Vorstand des Genetischen Instituts der Universität Helsinki, Herrn Professor Dr. HARRY FEDERLEY, bitte ich für die mir während der Ausführung der vorliegenden Untersuchung zuteil gewordene Hilfe meinen besten Dank auszusprechen.

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ZUR ZYTOLOGIE VON GODETIA-ARTEN UND -BASTARDEN

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LUND

(With a Summary in English)

DIE Systematik der Gattung *Godetia* ist schwierig, die Umgrenzung der Arten viel umstritten. Wild ist die Gattung in der Nähe der pazifischen Küste von Amerika; verschiedene Arten werden oft als Zierpflanzen kultiviert. HITCHCOCK hat neulich die nordamerikanischen Formen bearbeitet (HITCHCOCK, 1930). Dozent G. HIORTH in Ås, Norwegen, hat die Gattung in systematischer und genetischer Weise seit langem studiert und über die Arten der *amoena*-Gruppe berichtet (HIORTH, 1940). Das hier untersuchte Material stammt aus seinen Kulturen; es wurde in Ås fixiert. Die Fixierungen sind von cand. phil. ERIC RUNQUIST, Lund, ausgeführt; einige jedoch von HIORTH. Von HIORTH habe ich eine ausführliche Liste über das untersuchte Material bekommen. Bei der Fertigstellung des Manuskripts verwendete ich die Angaben und Bemerkungen, die HIORTH zu den verschiedenen Fixierungsnummern gemacht hat. Ich habe auch das Manuskript zu einer Abhandlung »Versuche mit *Godetia*-Arten» gesehen, in der HIORTH über die Systematik der zytologisch untersuchten Formen berichtet.

Es wurde die Meiosis der verschiedenen Formen studiert. Die somatischen Chromosomen wurden nicht in Wurzeln sondern nur im sterilen Gewebe der Blütenknospen studiert. Eingehende chromosomenmorphologische Beobachtungen sind also nicht angestellt worden. Für die Arten wurden Zahl, Grösse und Paarung der Chromosomen festgestellt, in den Artbastarden die Konjugationsaffinität der Chromosomen verschiedener Arten. Die Chromosomenzahlen von verschiedenen Godetien sind früher bekannt gewesen (HÅKANSSON, 1925; CHITTENDEN, 1928; JOHANSEN, 1929).

DIE AMOENA-GRUPPE.

HIORTH unterscheidet im westlichen Nordamerika die Arten *G. amoena*, *Whitneyi* und *nutans*. Ich habe zahlreiche von ihm gesammelte Formen untersucht und werde in einer anderen Abhandlung

meine Befunde vorlegen. Die Arten haben verhältnismässig grosse Chromosomen. Die Grundzahl ist 7. Die Bivalente haben in der Regel ein oder zwei terminale Chiasmen, aber bisweilen ist ein interstitielles Chiasma zwischen Centromer und Chromosomenende vorhanden. Bei diesen Arten ist dieses Chiasma subterminal, der am Bivalent gebildete

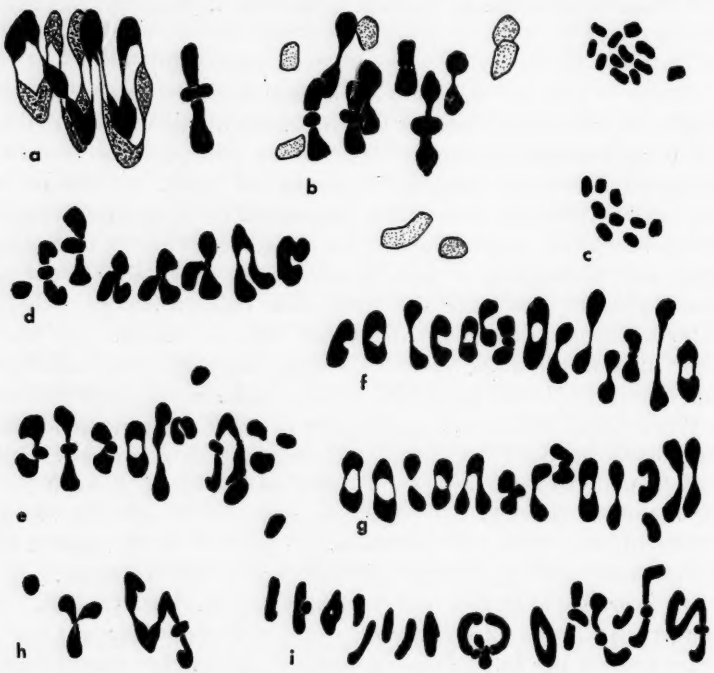

Fig. 1. — *a*: *G. Whitneyi* von Bear River Ridge, Cal. 12-Ring und Bivalent. × 3500. — *b*: *G. nutans* × *Whitneyi*. $7_{II} + 7_{I}$. × 3500. — *c*: *G. nutans* × *Whitneyi*. Metaphase 2. — *d*—*e*: *G. Whitneyi* × *amoena*, *3n*. — *d*: $6_{III} + 1_{II} + 1_{I}$. — *e*: $1_{III} + 6_{II} + 6_{I}$. — *f*—*h*: *G. Whitneyi* × *amoena*, *4n*. — *f*: 14_{II}. — *g*: $1_{III} + 12_{II} + 1_{I}$. — *h*: I + III + IV aus einer Kernplatte. — *i*: *G. tenella* × *Blauer Zwerg*. $2_{IV} + 12_{II} + 1_{I}$. × 3500. Wenn nicht anderes angegeben ist die Vergrösserung × 2000.

Querarm ganz kurz. Die Häufigkeit solcher subterminalen Chiasmen ist in vielen Formen sehr klein (HÅKANSSON, 1940 a), nicht eins pro PMZ, in anderen Fällen grösser, indem 2—3 der Bivalente in der diploiden PMZ einen Querarm haben.

G. amoena. n = 7. In wildwachsenden und kultivierten Formen.

G. Whitneyi. n = 7. Ich habe recht verschiedene Anordnungen

der Chromosomen in der Diakinese und ersten Metaphase bei wildwachsenden Typen gefunden. Einen Extremfall bildete eine Pflanze von Bear River Ridge, Humboldt Co., Cal., die nur ein Bivalent zeigte, die anderen 12 Chromosomen bildeten einen Ring (Fig. 1 *a*).

G. nutans. n = 14. 14_{II} zeigten Pflanzen von verschiedenen Fundorten. Dies stimmt mit den Kreuzungsergebnissen von HIORTH (siehe HIORTH, 1940).

G. Whitneyi × *amoena, 2n.* Der Bastard ist mehrere Male untersucht worden (HÅKANSSON, 1925; CHITTENDEN, 1928). Die meiotischen Teilungen waren sehr gestört, die Chromosomen aber gut gepaart, nur wenige oder gar keine Univalente schienen vorzukommen.

Eine neue Kombination, F 339'37, in der *Whitneyi* Mutterpflanze war, wurde untersucht. Die Teilungen waren regelmässiger als früher. Hier interessiert die Paarung der Chromosomen. Die gewöhnlichste Anordnung war $6_{II} + 2_{I}$. Recht häufig sah man 4 Univalente, eine etwas kleinere Zahl von PMZ hatten kein Univalent. Von den Bivalenten waren 0—2 ringförmig, eines hatte gewöhnlich ein subterminales Chiasma. Das *amoena*-Genom zeigte also gute, aber doch abgeschwächte Affinität zu dem *Whitneyi*-Genom.

Weiter kann erwähnt werden, dass die Univalente Grössenunterschiede zeigen können und dass die Bivalente gern in etwas ungleicher Höhe liegen.

G. Whitneyi × *amoena, 3n.* Den triploiden Bastard zwischen den beiden Arten hat HIORTH durch Bestäubung der autotetraploiden Mutante von *G. Whitneyi* mit Pollen von *G. amoena* hergestellt. Der Bastard (F 335'37) hat also zwei *Whitneyi*-Genome und ein Genom von *amoena.* Die Meiosis der autotriploiden *Whitneyi* habe ich früher untersucht (HÅKANSSON, 1940 a). Es kann also ein Vergleich zwischen der Auto- und Allotriploide gemacht werden.

Die Autotriploide bildete eine hohe Anzahl von Trivalenten. Univalente waren also selten. Die kleine Tabelle zeigt den Unterschied.

Univalente	0	1	2	3	4	5	6
Autotriploide 185	29	16	4	1	—	—	—
Allotriploide *Wh* × *a*	—	5	9	5	6	—	2

In der Diakinese wurden tri-, bi- und univalente Chromosomen beobachtet. Wie aus der ersten Metaphase hervorgeht, ist die Univalentenzahl höher. Während in der Autotriploide 7_{III} die häufigste Anordnung ist, ist sie $5_{III} + 2_{II} + 2_{I}$ in der Allotriploide. Während die

Zahl der Univalente bei der ersteren Form zwischen 0—3 schwankt, ist die Variation in der letzteren grösser, 1—6 (Fig. 1 *d* und *e*). Es bestätigt sich also hier, dass die Affinität der Chromosomen der beiden Arten gross, aber doch abgeschwächt ist. Es ist wohl wahrscheinlich, dass die Univalente meist *amoena*-Chromosomen sind. Ein deutlicher Grössenunterschied unter den Univalenten spricht auch dafür, da ein solcher im *amoena*-Genom deutlicher ist als in dem von *Whitneyi*.

Es wurden dieselben Trivalenttypen (7, 8 und 9) wie in der Autotriploide gefunden. In der ersten Anaphase waren Chromosomen oft verspätet und konnten eliminiert werden. Dies wurde aber auch bei der Autotriploide beobachtet und man kann nicht sagen, dass die meiotischen Teilungen in höherem Grad gestört sind.

G. Whitneyi × *amoena*, *4n*. Von HIORTH wurde ein fertiler *Whitneyi* × *amoena*-Bastard gefunden. Bei einer Kreuzung *Whitneyi 4n* und *amoena 3n* entstand in F_2 eine Pflanze von tetraploidem Habitus, die gute Pollenkörner hatte und diese gab nach Selbstung S 1035′40, eine Familie, die laut HIORTH aus Pflanzen von einheitlichem grossem und sehr kräftigem Typus mit gutem Pollen bestand.

Zwei Pflanzen der Familie S 1035′40 wurden untersucht. Sie waren tetraploid. Fig. 3 *a* zeigt die zweite Metaphase in der PMZ, in beiden Kernplatten sind 14 Chromosomen festzustellen. Die PMZ sind bedeutend grösser als bei dem triploiden Bastarde. In den somatischen Teilungen war die Chromosomenzahl dagegen nicht leicht zu bestimmen.

Das Material zum Studium der Chromosomenkonjugation war nicht gross und die Kernplatte konnte nicht oft vollständig analysiert werden. Es wurden einige Male 14_{II} beobachtet (Fig. 1 *f*). Einzelne Multivalente waren in der Platte jedoch in der Regel anzutreffen. Fig. 1 *g* zeigt $1_{III} + 12_{II} + 1_{I}$. Ein Quadrivalent kommt häufig vor, selten zwei oder mehrere. Bisweilen sieht man ein Univalent (Fig. 1 *h*). In der Anaphase war das Univalent verspätet und konnte eliminiert werden. Sonst waren die Teilungen sehr regelmässig.

Dieser Bastard zeigt also sehr wenig Quadrivalente (meistens nur eines). Ich habe früher eine tetraploide *Godetia* untersucht, eine autotetraploide *Whitneyi*-Mutante (HÅKANSSON, 1940 a). In dieser war die Paarung eine andere, mit meistens 5—7 Quadrivalenten in der PMZ. Mit Rücksicht auf die doch recht gute Affinität der *Whitneyi*- und *amoena*-Genome in den di- und triploiden Bastarden ist also die Multivalentbildung im tetraploiden Bastard sehr schwach. Eine Parallele haben wir aber z. B. in *Primula Kewensis*. Der diploide Bastard

P. floribunda × *verticillata* hat 9 Bivalente, Univalente sind nur zufällig vorhanden. Der tetraploide Bastard hat aber nur 2,4 Quadrivalente pro PMZ, sehr selten ein Trivalent-und-Univalent (UPCOTT, 1940).

G. nutans × *Whitneyi.* Bei meinen Studien über die westamerikanischen Godetien der *amoena*-Gruppe untersuchte ich einige Bastarde zwischen verschiedenen *nutans*- und *Whitneyi*-Typen. Hier soll kurz über die Chromosomenpaarung berichtet werden. S 308'40 waren Bastardpflanzen einer Kreuzung zwischen einer grossblütigen *nutans* aus Canyonville, Oregon (mit 14 Bivalenten) und einer *Whitneyi* aus Springfield, Oregon. Die Springfield-Pflanzen hatten 7_{II} oder $5_{II} + 4$-Ring oder $5_{II} + 1_{I} + 3$-Kette. Zwei Bastardpflanzen hatten $7_{II} + 7_{I}$, eine hatte $5_{II} + 4$-Ring $+ 7_{I}$. Die Bivalente und der Ring (es war häufig eine Kette) sehen wie in *Whitneyi* aus (Fig. 1 *b*). Zur Kreuzung wurde offenbar eine *Whitneyi*-Pflanze mit einem 4-Ring verwendet. Das Vorkommen von 7 Univalenten in den PMZ ist sehr konstant. Es wurden keine Trivalente beobachtet. *G. nutans* hat also ein Genom, das dem *Whitneyi*-Genom ganz homolog ist, und ein zweites, dessen Chromosomen zu den *Whitneyi*-Chromosomen gar keine Affinität zeigen.

Die Univalente liegen in der Kernspindel, und meistens ist nur eines von ihnen in der Platte. Infolgedessen kommen sie bei der Streckung der Spindel ungeteilt nach den Polen. Nur das in der Platte liegende ist bisweilen verspätet und kann eliminiert werden. In der zweiten Teilung sind meistens nur zwei Metaphaseplatten zu sehen (Fig. 1 *c*); ihre Chromosomenzahl lässt eine zufallsmässige Verteilung der Univalente vermuten. Trotz der grossen Anzahl von Univalenten sind die meiotischen Teilungen bei diesem Bastard also regelmässig, von der kleinen Elimination abgesehen.

Die Univalente haben verschiedene Grösse. Zwei von ihnen liegen gern dicht beisammen, vielleicht bestand zwischen ihnen in der Prophase eine Konnektion (Fig. 1 *b*). Die Bivalente befinden sich in etwas verschiedener Höhe; man bekommt den Eindruck, als ob die Platte sich langsam bildete.

S 310'40 war eine Kreuzung einer *nutans* von Glen Ellen, Sonoma Co., Cal., und einer kultivierten *Whitneyi*-Linie. Ich habe die Glen Ellen-*nutans* untersucht und fand Störungen der ersten Teilung. Es kommen zwar 14 Bivalente in der PMZ vor, aber oft findet man eine variierende Anzahl von Univalenten, die über die Kernspindel zerstreut liegen. Die Chromosomen in den Bivalenten trennen sich nämlich all-

mählich und ungleichzeitig, sodass immer mehr Univalente in der PMZ vorhanden sind und sich den Polen nähern. Schliesslich ist die ganze Spindel mit Univalenten bestreut, trotzdem von Anfang an nur Bivalente in der PMZ vorhanden waren.

Diese Eigenheit der ersten Anaphase zeigte auch der Bastard. Die Chromosomenanordnung ist in vielen PMZ $7_{II} + 7_{I}$. Es sind aber bald mehr Univalente 9, 11 bis 19 oder nur Univalente vorhanden. Die Bivalentchromosomen verhalten sich also wie in Glen Ellen-*nutans*, die Mutterpflanze des Bastards. Ihr Verhalten scheint genisch bedingt; und zwar handelt es sich um dominante Vererbung.

EINIGE DIPLOIDE ARTEN.

Die behandelten Arten sind nicht alle verwandt, es gibt auch Unterschiede in Anzahl und Grösse der Chromosomen. Fig. 2 *a* zeigt Beispiele von somatischen Chromosomen in den Fixierungsnummern. Auch ist von jeder der untersuchten Arten ein Bild der Chromosomen in der ersten meiotischen Metaphase wiedergegeben.

G. deflexa und *G. Bottae*. Diese Arten sind verwandt. HITCHCOCK fasst sie nicht als zwei verschiedene Arten auf. Er unterscheidet *G. Bottae* var. *typica*, diese ist schlank und hat schmale Blätter; *G. Bottae* var. *deflexa* ist robuster und hat breitere Blätter. Hier wurden untersucht:

F 313 war *G. deflexa*; sie wurde von HIORTH aus Samen von Dr. D. A. JOHANSEN, Palo Alto, Cal., und Dr. A. BALFOUR, Reading, England, erhalten.

$n = 9$. Die Chromosomen sind gross, grösser als in der *amoena*-Gruppe, PMZ messen 28 μ, sind also gross. Bivalente in der frühen Metaphase 1 zeigt Fig. 2 *b*. Sie haben ein oder zwei terminale Chiasmen; interstitielle Chiasmen sind selten. In der Diakinese sind aber solche in mehreren Bivalenten vorhanden, die Terminalisierung hat also seit der Diakinese fortgesetzt. Gegen Ende von Metaphase I haben die Bivalente im allgemeinen nur ein Chiasma, und die Anaphase setzte recht langsam ein. Einige Störungen wurden während den Teilungen beobachtet.

F 302. *G. deflexa*. (Aus Orange Co., Cal.) $2n = 18$. Es wurden nur somatische Teilungen studiert. Die Chromosomen waren recht gross; doch kleiner als in F 313 (Fig. 2 *a*).

F 314. *G. Bottae typica* (*G. Bottae* Lester Rowntree benannt, nach der Samenfirma in Carmel, Cal.). Laut HIORTH sehr abweichend in

Habitus und einigen Proben von *G. cylindrica* ähnlich; stimmte mit var. *typica* von HITCHCOCK überein.

n = 9. Die Chromosomen sind sehr klein, sie zählen zu den klein-

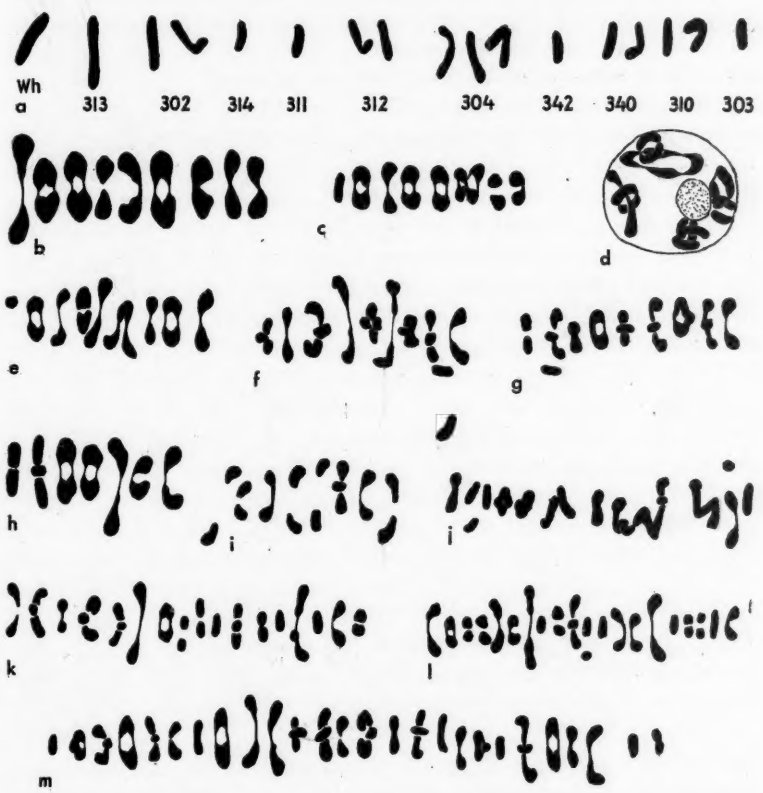

Fig. 2. — *a*: Somatische Chromosomen aus verschiedenen Fixierungsnummern. × 3500. — *b*: *G. deflexa*. 9_{II}. — *c—d*: *G. Bottae typica*. — *c*: 7_{II} + 4-Ring. — *d*: Diakinese. × 2000. — *e*: *G. parviflora*. $7_{II} + 1_I$ + 3-Kette. — *f—g*: *G. viminea*. — *f*: $9_{II} + 2_I$. — *g*: $9_{II} + 1_I$. — *h*: *G. hispidula*. 7_{II}. — *i*: *G.* »*biloba*». 8_{II}. — *j*: *G. tenella* × *Blauer Zwerg*. $1_{VI} + 1_{IV} + 10_{II} + 2_I$. — *k*: *Godetia*-Art aus Chile. 17_{II}. — *l*: *G. quadrivulnera*. Alle Chromosomen wurden nicht beobachtet. — *m*: *G. purpurea*. 26_{II}. Wenn nicht anderes angegeben ist die Vergrösserung × 2000.

sten der Gattung. Die PMZ messen 20 μ. Es gab sehr starke Terminalisation, interstitielle Chiasmen waren sehr selten. Im untersuchten Material war ein Ring aus vier Chromosomen vorhanden. In der

Diakinese war s. g. »interlocking» häufig (Fig. 2 *d*). Die Ringchromosomen sind in der ersten Metaphase zickzackorientiert, die Bivalente haben meist zwei terminale Chiasmen (Fig. 2 *c*).

Durch geringere Chromosomengrösse und kleinere PMZ unterscheidet sich F 314 von F 313. Weitere Untersuchungen müssen ent-

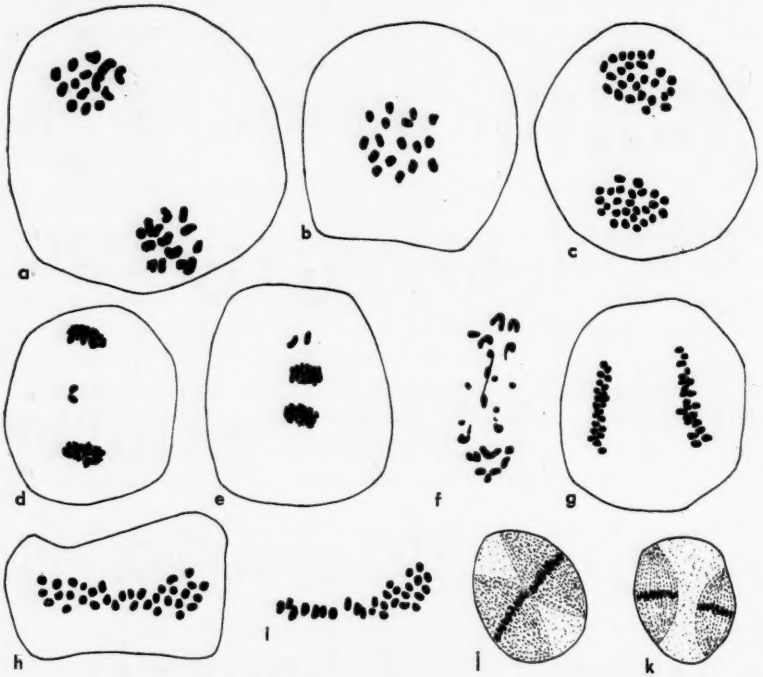

Fig. 3. — *a*: *G. Whitneyi* × *amoena*, *4n*. Metaphase 2. — *b*: *G.* »*dasycarpa*». Metaphase 1. — *c*: *G. quadrivulnera*. Metaphase 2. — *d*: *G. parviflora*. Anaphase 1, Elimination des Univalents. — *e*: *G. viminea*. Anaphase 1, Univalente früh nach dem Pole. — *f*—*j*: *G. tenella* × *Blauer Zwerg*. — *f*: Anaphase 1, sehr gestört. — *g*—*i*: Teilung 2, Vereinigung der Kernspindeln. — *j*: PMZ während Teilung 2. — *k*: *G.* »*dasycarpa*». Ditto. — *a*—*i*: × 1500.

scheiden, ob die kleinwüchsige *Bottae* var. *typica* immer kleine Chromosomen hat. Früher untersuchte *Bottae*-Pflanzen hatten grosse Chromosomen (HÅKANSSON, 1925; CHITTENDEN, 1928); CHITTENDEN hat sicher, ich wahrscheinlich var. *deflexa* untersucht. Das Vorkommen eines Rings hat keine artsystematische Bedeutung, es gehört der intra-

spezifischen Variation an, zeigt aber, dass ein Austausch zwischen nicht homologen Chromosomen auch in anderen Arten der Gattung als in der *amoena*-Gruppe vorkommt.

G. parviflora. F 311. Die Samen erhielt HIORTH von HITCHCOCK. Laut letztgenanntem Verfasser erscheint es unsicher, ob *parviflora* als eigene Art oder als Subspezies zu *viminea* aufzufassen ist.

n = 9. Die Chromosomen sind sehr klein, wie bei F 314. Die PMZ messen 20 μ. Die Bivalente sind sehr klein, haben ein oder zwei terminale, aber auch hier selten ein interstitielles Chiasma, das immer subterminal ist.

Die Chromosomenpaarung war in der untersuchten Pflanze recht eigentümlich. In der Diakinese und ersten Metaphase gab es $1_{III} + + 7_{II} + 1_{I}$. Das Trivalent bestand aus einer einfachen Kette (Fig. 2 *e*); nie wurde die verzweigte Kette oder der Ring mit Stab (Typus 8 und 9), die auch in der trisomischen *G. Whitneyi* vorkommen (HÅKANSSON, 1940 b), beobachtet. Man bekommt den Eindruck, dass das Trivalent nicht aus drei gleichen Chromosomen besteht sondern ein oder zwei strukturell veränderte Chromosomen hat. Es kann $a_1 . b_2$, $b_2 . b_1$, $b_1 . a_2$ oder $a_1 . a_2$, $a_2 . b_1$, $b_1 . b_2$ sein. Das Univalent ist nie mit anderen Chromosomen vereint und liegt in der Kernplatte (Fig. 2 *e*). Infolgedessen ist es in der Anaphase verspätet (Fig. 3 *d*). Die Verspätung kann mit sich bringen, dass es als Kleinkern eliminiert wird. Selten wurde seine Längsteilung oder Fragmentation beobachtet. Ein eliminiertes Chromosom wird in der zweiten Teilung geteilt.

Wie die Chromosomen in dieser Form zu deuten sind, bleibt ungewiss. Ich habe ganz dieselbe Anordnung mit einer 3-Kette und einem Univalent in einer *G. Whitneyi*-Pflanze aus Springfield gefunden. Es sieht aus, als ob eines der Chromosomen in einem 4-Ring sich nicht paaren könnte.

G. viminea. F 312 (Samen von Lester Rowntree). Stimmt nach HIORTH mit *viminea* von HITCHCOCK überein. Die hier untersuchten Pflanzen scheinen Bastarde zu sein.

n = 9. Es kommen nämlich 9 Bivalente vor. Die Chromosomen sind grösser als in F 311 und F 314, jedoch bedeutend kleiner und schmäler als in der *amoena*-Gruppe. Die PMZ messen 23 μ. Die untersuchten Pflanzen hatten 9 Bivalente und ein oder zwei Univalente (Fig. 2 *f* und *g*). Die Bivalente sehen etwas anders aus als bisher für *Godetia* beschrieben. Sie haben oft ein interstitielles Chiasma, das recht weit vom Chromosomenende ausgebildet ist; die gebildeten Querarme sind also bei dieser Art länger. Auch haben viele, 4—6 Bivalente,

einen Querarm. Die Metaphasenplatte hat in Seitenansicht ein ganz anderes Aussehen (vgl. Fig. 2 *f*).

Die Univalente zeigten keine Verwandtschaft zu den anderen Chromosomen. Sie verhalten sich wie im Bastard *nutans* × *Whitneyi* und nicht wie das Univalent in F 311. Sie sind meistens nicht in der Kernplatte, sondern liegen in verschiedener Weise in der Kernspindel und gelangen oft früh nach den Polen (Fig. 3 *e*). Eine Elimination ist selten und die Kernplatten der zweiten Teilung haben 9—11 Chromosomen.

Die beiden univalenten Chromosomen scheinen also artfremd zu sein, weshalb man vermuten kann, dass die reine *G. viminea* die 9 Bivalente besitzt. Die untersuchten Pflanzen scheinen aus einer Artkreuzung zwischen *G. viminea* und einer Art mit höherer Chromosomenzahl (17- oder 26-chromosomig) hervorgegangen zu sein. Es können keine Primärbastarde sein, aber vielleicht Rückkreuzungen mit *viminea*. Nach HITCHCOCK sind *parviflora* und *viminea* nahe verwandt, *viminea* hat aber etwas grössere Chromosomen, und die Bivalente haben ein anderes Aussehen als bei *parviflora*.

G. hispidula. F 304 (*hispidula*, Placerville, Eldorado Co., Cal.).

n = 7. Die Chromosomen sind recht gross, wie bei *deflexa* F 304. Die PMZ messen 20 μ. In der frühen Diakinese zeigen mehrere Bivalente ein nicht terminalisiertes Chiasma, die Bivalente ähneln jetzt denen von *deflexa*, aber nicht denen von *Whitneyi*. In der ersten Metaphase sind aber interstitielle Chiasmen meistens nur in einem oder in keinem Bivalent vorhanden (Fig. 2 *h*). Die Teilungen sind regelmässig.

G. hispidula hat also dieselbe Zahl wie die diploiden Arten der *amoena*-Gruppe, und die Chromosomengrösse ist auch ähnlich; abweichend war das Aussehen der Diakinese, die der in *deflexa* ähnelte.

G. »biloba». F 342 (aus Hell Hollow, Mariposa Co., Cal.; HIORTH hat die Samen von Dr. CARL WOLF erhalten, die Bestimmung wurde von HIORTH nicht näher kontrolliert). Ist nach HIORTH *Clarkia*-ähnlich oder gar eine *Godetia*-ähnliche *Clarkia*-Art.

n = 8. Die Chromosomen sind sehr klein, wie bei F 311 und F 314. Die PMZ sind trotz der geringen Chromatinmenge gross, sie messen 27 μ. Die Bivalente sind meistens stabförmig, nur eines hat in der Regel ein interstitielles Chiasma (Fig. 2 *i*). In einem Bivalent wurden die Chromosomen früh getrennt, im Bivalent mit dem subterminalen Chiasma trennten sie sich dagegen verspätet.

Die gefundene Zahl wurde in der Gattung früher nicht beobachtet. Sie scheint zytologisch recht isoliert zu sein.

DIE 17-CHROMOSOMIGE ARTGRUPPE.

Einige der untersuchten Formen hatten n = 17 Chromosomen (siehe Fig. 3 *b*). Es waren dies:

F 306 und *F 340*, »*Chile B*» bzw. »*Chile A*» (von Dr. GOODSPEED, Berkeley). Laut HIORTH zwei recht ähnliche Formen.

F 316, *Blauer Zwerg*, Gartenform von der Firma Ernst Benary, Erfurt, nach HIORTH *Chile B* sehr ähnlich.

F 315, *tenella* aus Brüssel. Diese Form wurde nicht untersucht, sie ist nach HIORTH wahrscheinlich von südamerikanischem Ursprung. Nach der Chromosomenzahl des Bastards *tenella* × *Blauer Zwerg* ist hier n = 17. CHITTENDEN gab aber für *tenella* n = 16 an.

F 310, *G.* »*dasycarpa*» (nach HIORTH *quadrivulnera-dasycarpa*, er erhielt sie aus einem botanischen Garten unter dem Namen *dasycarpa*). — (Nach HEGI, Illustrierte Flora von Mitteleuropa, ist *dasycarpa* in Oregon, California und Chile verbreitet.)

F 317. »Lavender Gem». 2n cirka 34.

Von F 306 und F 317 wurden nur somatische Teilungen studiert. Die Chromosomen sind klein, etwa wie bei F 312, aber grösser als bei F 314. Die PMZ sind kaum grösser als bei diploiden Formen, sie massen in F 316 23 μ. In der ersten und zweiten Metaphase ist die Chromosomenzahl leicht festzustellen (Fig. 3 *b*). Die Formen sind zytologisch recht ähnlich. In der Diakinese sind die Bivalente ringförmig, haben aber oft ein interstitielles Chiasma. In der ersten Metaphase haben die Bivalente oft einen Querarm, der gern recht lang ist. Die Bivalente von Chile A zeigt Fig. 2 *k*, sie sind denen von *viminea* ähnlich. Doch scheinen Unterschiede im Aussehen der Bivalente unter den verschiedenen Formen vorhanden zu sein. Multivalente wurden nicht beobachtet, einzelne Univalente kommen doch selten vor.

Die Formen dieser Gruppe stammen aus Südamerika oder von südamerikanischen Formen ab (»*dasycarpa*»?).

G. tenella × *Blauer Zwerg* (F 336) und reziprok (F 337). HIORTH hat die Bastarde hergestellt, sie haben nach ihm schlechten Pollen, nur einzelne Pollenkörner waren gut entwickelt und 5- oder 6-lappig. Ich fand auch, dass recht viele Pollendiaden gebildet werden; ihre Anzahl war in den Kleinfächern der Antheren sehr verschieden, bisweilen wurden $^1/_3$ Diaden konstatiert. Bildung von Diaden durch Teilung eines Restitutionskerns habe ich bei mehreren Godetien beobachtet. Diese Bastarde haben aber nur wenige Univalente und bilden nicht Restitutionskerne; Störungen in der zweiter Teilung sind dagegen häufig.

Es kann hier ihre Zytologie nur kurz behandelt werden. Wie aus der Diakinese und ersten Metaphase hervorgeht, ist die Chromosomenpaarung gut. Es gab nur 0—4 Univalente, recht häufig waren zwei Univalente in der PMZ. Einige Multivalente waren in den Platten recht gewöhnlich, die Platten konnten aber nur selten vollständig analysiert werden, da es sehr schwierig ist, alle Chromosomen in Seitenansicht zu unterscheiden. Fig. 1 *i* zeigt $2_{IV} + 12_{II} + 1_{I}$ (oder $2_{IV} + 2_{III} + 10_{II}$), Fig. 2 *j* $1_{VI} + 1_{IV} + 10_{II} + 2_{I}$. Die Zahl der Multivalente ist doch klein, es scheint, als gebe es meistens nur ein Quadrivalent.

Nach der Anaphase werden zwei Interkinesekerne gebildet. Die Anaphase ist meistens regelmässig, wie aber Fig. 3 *f* zeigt, können bisweilen Brückenbildungen und Fragmente vorkommen; es ist aber nicht sicher, dass sie hier auf Inversionen in den Chromosomen deuten. Eine Elimination von Univalenten kann vorkommen.

Die zweite Teilung ist oft sehr regelmässig. Die beiden Kernspindeln sind aber ungewöhnlich breit, sodass sie sich in der Mitte berühren (Fig. 3 *j*). Bei den Arten ist dagegen immer Zytoplasma zwischen den Spindeln (Fig. 3 *k*). Es trat nun bisweilen ein Chromosom von der einen in die andere Kernspindel über, und es kam zu einer Vereinigung von zwei Metaphase- oder zwei Anaphasegruppen. Quergeschnittene Platten sind dann stundenglasförmig und können 34 Chromosomen zeigen (Fig. 3 *h*). Die Vereinigung einer quer- und einer längsgestellten Spindel zeigt Fig. 3 *i*. Es werden also nicht selten zwei statt vier Kerne gebildet (Fig. 3 *g*), die die somatische Chromosomenzahl haben. Die erwähnten Pollendiaden werden also nach einer Vereinigung der beiden Spindeln der zweiten Teilung gebildet.

Die Chromosomen von *tenella* und *Blauer Zwerg* zeigen also in Bastarden gute Paarung. Das Vorkommen von Multivalenten deutet doch auf gewisse strukturelle Unterschiede in den Chromosomen der beiden gekreuzten Formen.

DIE 26-CHROMOSOMIGE ARTGRUPPE.

Einige der untersuchten Formen haben die Chromosomenzahl $n = 26$. Es waren *G. quadrivulnera* und *G. purpurea* (Fig. 3 *c*). CHITTENDEN hat diese Zahl früher für *G. lepida* angegeben, laut HIORTH hat CHITTENDEN aber *G. purpurea* untersucht.

F 305, *quadrivulnera* (Grants Pass, Oregon).

F 308, *quadrivulnera* (Dr. D. A. JOHANSEN).

F 309, *quadrivulnera* (von HIORTH unter der Bezeichnung *goddardi* von Lester Rowntree erhalten). 2n cirka 52.

F 341, *quadrivulnera* (Glen Ellen, Sonoma Co., Cal.).

F 303, *purpurea*, Glen Ellen. Genau derselbe Fundort wie für F 341. Laut HIORTH entweder eine *purpurea*-Form oder eine *quadrivulnera*-Form mit mehreren Merkmalen von *purpurea*.

F 307, *purpurea*, typisch. Eine Form, die in vielen botanischen Gärten vorkommt, bildet mit gewissen *quadrivulnera*-Formen fertile Bastarde.

F 301, *quadrivulnera*, Placerville, Eldorado Co., Cal. Man könnte diese sehr variable Form nach HIORTH zu *G. viminea*, *G. quadrivulnera* oder *G. purpurea* bestimmen.

Es wurde F 309 nur somatisch studiert. Die Chromosomen dieser Formen sind klein, von kleinsten Typus. Die PMZ messen 21—28 μ, haben also kaum eine Vergrösserung erfahren; nähere Studien wurden nicht gemacht. Die Chromosomenzahl ist leicht in den regelmässigen meiotischen Teilungen festzustellen (Fig. 3 *c*). Es kommen 26 Bivalente vor (Fig. 2 *m*). Die Figur stellt *purpurea* (F 303) dar, die Bivalente sind hier wie bei *viminea* und 17-chromosomigen Formen; sie haben häufig einen recht langen Querarm. Fig. 2 *l* zeigt die meisten Bivalente von *quadrivulnera* F 341 (also von demselben Fundort wie F 303); bei dieser Form wurden interstitielle Chiasmen weniger häufig ausgebildet. Es wurde aber nicht zu bestimmen versucht, ob im Aussehen der Bivalente zwischen den verschiedenen Fixierungsnummern konstante Unterschiede vorhanden waren. Univalente wurden bisweilen beobachtet (Fig. 2 *l*), dagegen keine Multivalente.

G. quadrivulnera ist eine sehr formenreiche Art. Nach HITCHCOCK ist es »the most widespread, as well as the most variable species of the genus». JOHANSEN gab die Chromosomenzahl zu $2n = 14$ an.

ALLGEMEINER TEIL.

Von *Godetia* gibt es »diploide» Arten mit der Chromosomenzahl 7, 8 oder 9 und »polyploide» mit 14, 17 oder 26 Chromosomen. Nur *G. nutans* zeigte Verdoppelung einer Grundzahl.

Pseudohexaploid waren *G. quadrivulnera* und *purpurea*. Die erstgenannte Art hat in der Gattung die grösste Verbreitung von allen und zeigt die grösste Variation. Die von mir untersuchten Typen hatten jedoch alle 26 Chromosomen. Wie in *purpurea* sind die Chromosomen sehr klein. Die Zahl 26 zeigt, dass kaum Autopolyploidie vorliegen

kann. Es sind aber recht viele Arten mit 9 und 17 Chromosomen in der Gattung, weshalb es nahe liegt anzunehmen, dass eine 9-chromosomige und eine 17-chromosomige Art einen Bastard bildeten, aus dem nach Chromosomenverdoppelung eine Form mit 26 Chromosomen entstanden ist. Bildung von Pollenkörnern mit der somatischen Zahl habe ich für mehrere Formen beschrieben. Es ist also eine allopolyploide Herkunft anzunehmen. HITCHCOCK veröffentlicht in seiner Abhandlung einen Stammbaum der *Godetia*-Arten. *Quadrivulnera* und *purpurea* stehen an der Basis des Baumes. Dies kann nicht die wahre Verwandtschaft der Arten angeben. Es sind dies später entstandene Formen und es ist wohl wahrscheinlich, dass 26-chromosomige Arten mehrmals entstanden sind.

Eine zytologisch einheitliche Gruppe bilden auch die Pseudotetraploiden. Es waren Arten aus Chile oder mit diesen verwandte Formen. Hier konnte die Verwandtschaft der Genome im Bastard zwischen *G. tenella* und der Gartenform *Blauer Zwerg* geprüft werden. Die Paarung war gut und zeigte Ähnlichkeit mit der im tetraploiden *Whitneyi* × *amoena*-Bastard. Einige strukturelle Verschiedenheiten scheinen in den Chromosomen der beiden gekreuzten Formen vorhanden, Asyndese kommt aber nur wenig vor (0—4 Univalente). Man kann damit die Chromosomenverhältnisse im Bastard zwischen *G. deflexa* und *Whitneyi* vergleichen, also zwei Arten, die nicht verwandt sind. Ich habe meine Untersuchungen noch nicht veröffentlicht, will aber mitteilen, dass sie vollständige Asyndese zeigten: in der Diakinese und ersten Metaphase waren nur Univalente vorhanden. Trotz der guten Paarung bildete aber der *tenella* × *Blauer Zwerg*-Bastard recht viele Pollenkörner mit der somatischen Chromosomenzahl. Die beiden Kernspindeln der zweiten Teilung bildeten nämlich nicht selten zwei statt vier Kerne. In anderen Godetien führt dagegen Asyndese zur Bildung von Restitutionskernen und Pollenkörnern mit der somatischen Zahl. Die Zahl 17 lässt auch hier Allopolyploidie vermuten.

G. nutans gehört der *amoena*-Gruppe an. In dieser finden sich zwei diploide Arten, *amoena* und *Whitneyi*. Die Verwandtschaft ihrer Chromosomen konnte in di- und triploiden Bastardpflanzen studiert werden. Die Genome der beiden Arten zeigen gute aber etwas abgeschwächte Affinität. Es fragt sich, ob die tetraploide *G. nutans* auto- oder allopolyploid ist. Sie hat nur Bivalente aber keine Multivalente. Eine Untersuchung der Chromosomenpaarung im Bastard zwischen *nutans* und *Whitneyi* zeigt, dass *nutans* ein Genom hat, das mit dem Genom von *Whitneyi* übereinstimmt. Das zweite *nutans*-Genom ist

aber ganz verschieden und zeigt keine Verwandtschaft mit dem ersten. Aus der Paarung im Bastard geht also hervor, dass auch *G. nutans* allopolyploid ist.

Die Herkunft des zweiten Genoms ist aber ungewiss. Man könnte vermuten, dass es von der anderen diploiden Art der Gruppe, *amoena*, stammt. Ich habe einen von HIORTH erhaltenen tetraploiden Bastard *Whitneyi* × *amoena* untersucht. Während *nutans* immer 14_{II} in den PMZ hat, hat dieser Bastard zwar bisweilen 14_{II}, meistens sind aber in den PMZ einzelne Multivalente vorhanden. Der Unterschied in der Paarung ist also nicht gross. Ein grosser Unterschied besteht aber zwischen dem triploiden *Whitneyi* × *amoena*-Bastard (= 4n *Whitneyi* × 2n *amoena*) und *nutans* × *Whitneyi*. Beide Bastarde sind triploid und haben zwei *Whitneyi*-Genome. Das dritte Genom kommt im erstgenannten Bastard von *amoena*, im anderen ist es unbekannt. Der eine Bastard bildet 1—6 Trivalente, der andere nie Trivalente. Letzterer kann also kaum das *amoena*-Genom besitzen, das zweite *nutans*-Genom muss von einer unbekannten Art stammen.

In der *G. amoena*-Gruppe zeigt also das Genom von *amoena* Verwandtschaft zu dem Genom von *Whitneyi*, und das letztere Genom ist in *nutans* vorhanden. Die Grösse der Chromosomen und das Aussehen der Bivalente sind in den Arten ähnlich, sie scheinen also verwandt zu sein.

Es scheint also, als wäre in der Gattung Allo- eher als Autopolyploidie wirksam. In *Godetia* kommt Autopolyploidie in *Whitneyi* vor (HÅKANSSON, 1940 a), ihre Bedeutung für die Formbildung in der Natur ist aber ungewiss.

Strukturelle Veränderungen der Chromosomen scheinen häufig zu sein, dies geht aus Ringbildungen in spontanen Formen und aus Meiosis von Artbastarden hervor. Ihre Häufigkeit in *G. Whitneyi* ist früher hervorgehoben (HÅKANSSON, 1940 a). Es wurde jetzt ein Chromosomenring in *G. Bottae* var. *typica* gefunden, und die untersuchte Pflanze von *G. parviflora* zeigte eine Chromosomenpaarung, die sie als strukturellen Bastard erkennen lässt. Wie angedeutet, gibt es auch unter den Arten mit 17 Chromosomen strukturelle Verschiedenheiten.

Die Chromosomengrösse ist verschieden, in der 26-chromosomigen Artgruppe sind die Chromosomen sehr klein, in der 17-chromosomigen etwas grösser, während die Arten der *amoena*-Gruppe grosse Chromosomen haben. Es ist doch etwas ungewiss, ob die Grössenunterschiede in den anderen Arten systematisch so bedeutungsvoll sind. Unter diesen hatten *Bottae*, *deflexa*, *parviflora* und *viminea* 9, »*biloba*» 8 und

hispidula 7 Chromosomen. *Bottae* und *deflexa* sind verwandt, zeigen aber extreme Unterschiede in der Chromosomengrösse. Es schien hier aber eine Parallelität zwischen Chromatinmenge, Grösse der PMZ und Habitus zu geben, indem die zartere *Bottae typica* sehr kleine Chromosomen und kleinere PMZ besass.

Parviflora und *viminea* sind nach HITCHCOCK verwandt, die Zahl 9 kommt somit in zwei verschiedenen Verwandtschaftskreisen, *Bottae-deflexa* und *parviflora-viminea*, vor. Zytologische Unterschiede zwischen diesen Kreisen wurden nicht beobachtet, grösser scheinen sie innerhalb der Kreise zu sein. In bezug auf Chromosomengrösse stimmt *parviflora* mit *Bottae typica* überein, *viminea* hatte etwas grössere Chromosomen wie die 17-chromosomigen Arten. Die Bivalente von *viminea* haben ein anderes Aussehen als in den anderen diploiden Arten. Sie zeigen eine schwächere Terminalisierung von Chiasmen, sie haben darum oft recht lange Querarme. Auch in dieser Hinsicht zeigt *viminea* Ähnlichkeit mit Arten der 17-chromosomigen Gruppe, und übrigens auch mit solchen der 26-chromosomigen. Es soll aber hinzugefügt werden, dass nicht reine *viminea*, sondern Pflanzen untersucht wurden, die wahrscheinlich aus einer Kreuzung zwischen *viminea* und einer höherchromosomigen Art hervorgegangen sind.

G. »*biloba*» ist in der Gattung zytologisch isoliert. Die Zahl 8 kommt in keiner anderen Form vor, die Chromosomen sind sehr klein, sodass die Chromatinmenge der Zellen gering ist, trotzdem sind die PMZ gross, beinahe ebenso gross wie bei *deflexa* mit ihren neun grossen Chromosomen. *G. hispidula* zeigte gewisse zytologische Ähnlichkeiten mit der *amoena*-Gruppe, aber auch mit *deflexa*.

SUMMARY.

Meiosis in species and species hybrids of *Godetia* was studied. The investigated plants were grown by Dr. GUNNAR HIORTH in Ås, Norway.

Wild-growing species of the *amoena*-group (cf. HIORTH, 1940) have rather large chromosomes; their bivalents show one or two terminal chiasmata and occasionally a subterminal chiasma. *G. amoena* and *Whitneyi* have 7, *nutans* 14 chromosomes. A *Whitneyi* plant with 12-ring and one bivalent was found.

In diploid *Whitneyi* × *amoena* hybrids the chromosomes show good pairing. In a triploid hybrid with two *Whitneyi* and one *amoena* genome there are 1—6 trivalents. The triploid hybrid *nutans* × *Whitneyi* has no trivalents, the chromosome pairing is $7_{II} + 7_{I}$. One genome in

nutans is homologous with the *Whitneyi* genome, the other genome is different, it seems it does not belong to *amoena*.

The chromosomes separate in a peculiar manner at first meta-anaphase in a *nutans* from Glen Ellen, Sonoma Co., Cal. Hybrid plants, F_1 *nutans* Glen Ellen × *Whitneyi*, showed the same behaviour of the bivalent chromosomes, which seems to be genotypically controlled.

A tetraploid hybrid *Whitneyi* × *amoena* was also investigated. Some pmc:s had 14_{II}, a few multivalents were, however, often observed. The divisions are regular, a lagging univalent may be seen in the anaphase.

G. deflexa and *Bottae typica* have n = 9. The robust *deflexa* has large chromosomes, the slender *Bottae typica* very small chromosomes.

G. parviflora and *viminea* also have n = 9. The chromosomes of *parviflora* are very small, those of *viminea* are larger. The bivalents of *parviflora* seldom have a subterminal chiasma, the bivalents of *viminea* have often a chiasma between the centromere and the end of the chromosomes. The investigated *parviflora* plant was presumably a structural hybrid and showed 7 bivalents + univalent + chain of three, the univalent lagging at first anaphase. The investigated *viminea* plants were presumably derived from a cross between *viminea* and a species with a higher chromosome number; they showed a few univalents which do not lag.

A group of forms from Chile or related to the Chilean forms had 17_{II}. In form and size the bivalents were similar to those in *viminea*. Hybrids between *tenella* and *Blauer Zwerg* had good chromosome pairing; a few multivalents indicated structural differences, the spindles of the second division being broad and sometimes fused, forming dyad nuclei with 34 chromosomes.

Several forms of *G. quadrivulnera* and *purpurea* had 26 bivalents. Their chromosomes were small. This chromosome number has perhaps arisen through crosses between species with 17 and 9 chromosomes.

G. hispidula had 7 rather large chromosomes.

G. »biloba» had 8 chromosomes. They are small, but the species has rather large pmc:s.

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PRELIMINARY YIELD EXPERIMENTS WITH TEN INDUCED MUTATIONS IN BARLEY

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INDUCED VITAL MUTATIONS.

AT an irradiation of 25000 to 30000 r-units seeds of wheat, oats and barley will be so heavily bombarded as to display mitotic irregularities in almost every cell (FRÖIER, GELIN and GUSTAFSSON, 1941). Consequently all possible kinds of intra- and intergenic alterations arise. Chromosome breaks, distributed all over the genome, will produce profound structural rearrangements. Simultaneously, intragenic changes will appear, either conditioned by a chemical or physical influence on radicals and atoms in the gene molecule or passively by a break, with the wound subsequently healing, close to or inside the gene. According to DEMEREC's studies (1937) on the relationship between lethals, deficiencies and structural rearrangements, recessive visible mutations in *Drosophila* arise independently of breaks. This makes it probable that so-called gene mutations in fact result from direct or secondary X-ray effects irrespective of any processes of breakage.

Induced mutations in cereals are especially frequent *close to the lethal point of X-rayed seeds*, where cell divisions contain about 100 % disturbances (fragments and bridges) and the kernels germinate in field experiments to about 10 or 20 %. The chimæric structure, created after such a heavy irradiation, is the result of selection processes, cells with profound deletions and two-centromere formations disappearing rapidly. At the time of meiosis, however, an immense multitude of gene mutations, deficiencies, duplications, translocations and inversions are still present. Gametes, arisen after the irregular X_1 meiosis, receive all kinds of balanced and unbalanced genotypes, among which the lethal ones immediately vanish.

Non-lethal gene mutations and structural rearrangements frequently combine in the progeny, and an intentional selection may take place. The plant-breeder can choose at will among the realized new genes and rearrangements. But there still remains the difficult task of selectioning valuable biotypes and lines.

This schematic program can be exemplified in the following manner.

In the spring of 1937 seeds of Golden barley stored from 1931 were irradiated. 30 X_1 plants resulted (= 5,9 %), having an average sterility of 68 %. One of these X_1 plants differed from the others in having a new type of ear (a semidominant—dominant mutation). From 34 spikelets one seed arose (the plant sterility = 97 %), giving rise to an *erectum*-like mutation in the X_2 generation (GUSTAFSSON, 1941). This single plant produced in the next generation a family which appeared constant in ear-type, leaf-breadth and seed-characters. The mutation cannot be an admixture, since the X_1 plant was highly sterile and already changed and, further, the mutation differs from all *erectum* varieties cultivated in Sweden. From the most common strains, Svanhals and Primus (I and II), it is distinguished by the erect ear and delayed ripening (this from Svanhals), and by the long hairs at the rachilla (this from Primus), as well as in a series of other properties. Besides, it differs from all examined *erectum* barleys by the dominance of the transverse nick at the base of the seed (cf. TEDIN and TEDIN, 1927). The mutation, if crossed to Golden barley, gives an F_1 having the transverse nick instead of a bevelled seed surface, usually appearing in crosses between *erectum* and *nutans* lines.

At the time of X-radiation most seeds of this series were so damaged that they were unable to survive. In a few seeds, however, mitosis was apparently less deranged, leading to daughter-cells capable of repeated mitosis. Simultaneously gene mutations were frequently produced. In one embryo a dominant or semidominant mutation arose, later influencing the phenotype (the ear) in a heterozygous condition. Owing to the intense structural rearrangements, meiosis of the few resulting plants was irregular and disordered. This was especially the case in the X_1 plant heterozygous for the (semi-)dominant mutation. Here chromosome disturbances were so profound (97 % sterility) that most gametes died, but two identical or similar, intensely changed genotypes happened to combine, where gene mutation and rearrangements were in harmony. Consequently in X_3 a uniform or fairly uniform family was obtained.

Another example is described by GUSTAFSSON, 1940 and 1941. In a special seed series 505 kernels of Golden barley were irradiated. 30 resulting X_1 plants (= 6 %) had an average sterility of 70 %. 10 chlorophyll mutations, 4 sublethal mutations and 6—7 (morphological or) physiological, vital mutations were discovered in the X_2 and X_3

generations, corresponding to a minimum mutation frequency of 70 %. In this series the number of chromosome disturbances was directly examined in the first mitotic cycle of the germinating seeds and found to be at least 71 %, probably close to 100 %. No doubt, the genome has been entirely split up by the X-radiation. In later generations ($X_2 \ldots\ldots X_n$) the structural heterozygosity was broken up into a number of vital structural homozygotes, sometimes different from, but if gene mutations did not appear, most frequently phenotypically identical or very similar to the original line.

A plant-breeder anxious to obtain a great number of viable mutations should irradiate dormant seeds so intensely as to decrease germination from 95 % to 10 or 20 % (i. e. in cereals use a dose of 20000—30000 r), simultaneously producing frequent gene mutations and a profound structural differentiation. An irradiation of seeds should, in the writer's opinion, be superior to a treatment of pollen grains and egg cells owing to the long time of selection in seedling, ear and gamete stages.

WHAT TYPES OF MUTATION ARISE AFTER IRRADIATION?

In barley the same results have been obtained as in other carefully studied organisms, as for instance *Drosophila*. A detailed report was published by the writer in 1941. SMITH (1939) described a series of lethal and viable X-ray mutations in another plant species, *Triticum monococcum*. Among lethal and sublethal types in barley chlorophyll mutations of various kinds, dwarfs and sterility mutations are especially frequent but lines susceptible to diseases also occur.

Of greater practical interest, however, are the vital mutations, the most common group of which consists of so-called *erectoides* types. Altogether 12 or 13 cases of such mutations have been observed so far by the writer. Most of them are easily distinguished from the mother strain (Golden barley) by the dense ears and resemble in appearance the *erectum* barleys, already in cultivation, but only one mutation possesses the transverse nick at the seed-base so characteristic of the true *erectum* types.

Other mutations repeatedly obtained are the *six-row* and the *winter* barleys, observed three and two times respectively. A morphological mutation, *changing the glumes* to a lemma-like shape, arose twice. Mutations influencing *kernel colour* and *kernel size* are fairly

common, likewise *straw-height* and *straw-stiffness* mutations. Variations respecting *time of maturity* are frequently found, especially in the direction of a prolonged vegetative period, although mutations in the direction of increased earliness have also been noted.

These are just a few types of morphological and physiological interest discovered in barley. In a later chapter mutations changing yield and chemical properties will be described. It can now be regarded as definitely established that a pure line or a variety can be split up in many directions by means of X-rays, creating a vast field of possibilities to plant-breeding. There are no longer any grounds for the scepticism expressed by STADLER in 1930.

ARE PROGRESSIVE MUTATIONS PRODUCED BY X-RAYS?

A general definition of the term »progressive» will be given later on. Here we shall confine ourselves to a discussion of the significance of mutations for plant-breeding. One very pertinent problem concerns their individual phenotypic properties. Essentially it does not matter very much if mutations are less productive than their mother strain, provided they acquire qualities of value from other points of view. If, for instance, barley mutations arose, capable of enduring an increased fertilization owing to a superior straw-stiffness, or possessing a very high nitrogen content in the seeds, these improvements would for certain purposes counterbalance a small decrease in yield under normal conditions. Or — to take another example — if earliness mutations become suddenly available in soya beans or in sweet lupins, increasing the area of cultivation northwards or towards inhospitable climatic regions in general, this may be of importance to a country where the species was previously unable to grow. In these instances, however, the induced mutations are preponderantly of indirect value. The conclusive test of the significance of mutations for plant-breeding would be afforded by lines or families, improving individual properties without any decrease in production, or even improving and increasing the yield.

Among the erectoides mutations, briefly described by NILSSON-EHLE in 1939, one was equal in production to Golden barley (the mother strain) and endured, owing to its straw-stiffness, an increased fertilization. The present writer produced a series of different vital mutations in the years of 1937—1939. In order to test their value a yield trial was performed in 1940, covering ten different mutations, the mother

strain (Golden barley) and the highest-yielding commercial variety in Scandinavia (Maja barley). The preliminary experiments showed — even if an accurate evaluation of all details must be postponed — that irradiation will produce mutations, usually inferior, but not infrequently equal in production or even superior to the mother line. One or two mutations attained the level of Maja barley.

A similar result was reported by TIMOFÉEFF-RESSOVSKY (1935) in *Drosophila melanogaster*. Among sex-linked mutations produced by X-rays, lethals and semilethals were very common, but mutations having minor deleterious effects were even more frequent than lethals and semilethals combined. One variation, increasing viability, was tested in further generations and found to be hereditary. As a measure of viability TIMOFÉEFF-RESSOVSKY used the competition of males and females in ClB-progenies (»relative vitality»), the proportion normally being approximately 1 : 2, but when lethals or semilethals are present 0—0,30 : 2, when minor deleterious mutations are in operation, 0,30—0,80 : 2 and, finally, when modifiers increase the relative vitality, $> 1 : 2$.

YIELD EXPERIMENTS.

The following is a description of the barley varieties used and the induced mutations tested in comparative yield trials.

Gullkorn (Golden barley) was isolated already in 1897 by means of the pedigree method from one single plant of a Swedish local strain. It belongs to the lax-eared varieties (*Hordeum nutans*), like, for instance, the old barley varieties Prinsess, Hannchen and Chevalier, the rachilla is long-haired and the side-nerves of the seeds covered with barbs (β-type according to the system of ATTERBERG, 1899). Due to a series of accidents it was not put on the market until 1913, but continued until about ten years ago to be of great commercial importance. It is still cultivated, although to a small extent, in certain districts of South-eastern Sweden. For the last ten years it has been displaced by the Danish varieties Kenia, Opal and *Maja*, all of which are cross-products of Gullkorn and Binder (a pedigree of Mohravia barley). In the original Danish yield trials Golden barley gave approximately 10 % less return than Maja barley. The straw-stiffness is very much improved in Kenia and Maja, although Kenia is definitely superior to Maja in this respect. Frequently, and especially after an intense manuring, Golden barley is lodging. No conspicuous differences regarding earliness exist, and Maja, as well as Golden barley, ripen early.

Of the mutations produced in 1937—1939 about fifteen types appeared so vital that a thorough comparison between them and Golden barley seemed desirable. Besides being vital (i. e. even in field experiments germinating up to 100 %, growing fast, tillering intensely and giving a high grain production), every one of them was completely fertile, certainly not more than two or three embryos in a hundred being dead and undeveloped. In 1940 fairly good seed material was available for sowing from the following vital mutations:

Erectoides 1 (1939: 13: 22). Arose in 1937 after an irradiation in 1936 of aged, moistured seed material (1931 B III 1 $^1/_2$ h. water). Of 71 sown seeds 47 (= 66 %) germinated, and 32 full-grown plants were obtained. In laboratory experiments (1936—1937) halves of each ear from these 32 X_1 plants were examined with regard to the number of chlorophyll mutations. The mutation frequency in X_2 was 19 %. Of all ears, one half of which gave a chlorophyll mutation in the laboratory, the other half was examined in field experiments (1937). Here an *erectum*-like type »with very dense ear» was discovered. In the same ear-progeny a *xantha*-mutation occurred.

Erectoides 2 (1939: 13: 38). Was discovered in 1937. In 1936 seeds of the series 1934: A IV dry were irradiated. Of 260 treated seeds 239 (= 93 %) germinated, and 195 full-grown plants were obtained. The frequency of chlorophyll mutations in laboratory experiments was determined in the same manner as in the previous case (6 %). Two plants out of six in an X_2 ear-progeny were recorded as »densely eared».

Erectoides 3 (1939: 14: 1). Discovered in 1937—1938 as a semi-dominant mutation in X_1 by Mr. C. G. VON SYDOW. Aged seed material (1931 B IX dry) was irradiated in 1937. 30 full-grown plants arose from 510 sown seeds (6 %). X_3 material descending from seven different X_1 plants and X_1 ears was examined in 1939. Three cases of chlorophyll mutations were found. In 1940 further field material was sown, descendants of 27 different X_1 ears and 25 X_1 plants examined in all. From the 25 X_1 progenies 5 chlorophyll mutations originated (the mutation frequency = 20 %). In addition to erectoides 3 a morphological mutation having lemma-like glumes segregated (in 1940). Presumably one or two more ear and straw-stiffness mutations were found. The mutated X_1 plant (97 % sterile) was described as »broad- and dense-eared».

Erectoides 4 (1939: 14: 9). Found in an X_2 generation (1938). 645 seeds desiccated above concentrated H_2SO_4 were irradiated, and

55 full-grown plants (= 8 %) arose. The immediate germination percentage equalled 22. The sterility of the mutated X_1 plant was 37 %. The progeny of one entire X_1 ear (20 seeds) proved homozygous for the mutation. (»All plants *erectum*-like but not especially dense-eared.») The frequency of chlorophyll mutations in laboratory X_3 cultures was 16 %. In the X_2 generation two erectoides, one straw-stiffness (?, not controlled in further generations) and one glume mutation (the glumes lemma-like) were discovered. In 1940 a great X_3 generation was further examined. One six-row mutation and four more probable cases of erectoides and straw-stiffness mutations arose. Thus at least five, probably more, vital mutations were found in this series.

Erectoides 5 (1939: 14: 20). From the same series as erectoides 4. Discovered in 1938. The X_1 sterility was 55 %. Even here the progeny of an entire X_1 ear proved homozygous for the mutation. »Ears not quite *erectum*-like. The lowest kernels not very projecting. Straw-stiffer than Golden barley.»

A mutation with lemma-like glumes (1939: 14: 32). From the same series as erectoides 4 and 5. Found in the X_2 generation (1938). Plant sterility = 83 %. Six X_2 plants were mutated, two were Golden barley. »Four-rowed?» (Mr. C. G. VON SYDOW).

Late mutation (1939: 13: 65). Aged seeds (1932 B dry) were irradiated in 1935. Discovered in 1937 in the X_3 generation. Four X_3 pedigrees were homozygous for the mutation. All segregated for a chlorophyll mutation (*alboviridis—albina*). X_2 consisted of 8 plants (6 green : 2 *alboviridis*), originating from one half of an X_1 ear. »Five days later than Golden barley.»

Leaf-colour mutation (1939: 5: 9). Discovered in the X_3 (1939). The X_1 plant had a sterility of 43 %. One *albina* and one *xantha* mutation arose in the same plant progeny. 505 seeds, desiccated above concentrated H_2SO_4 and irradiated, gave 30 full-grown plants (= 6 %). The immediate germination was 14 %. This series (1937: 110) has been previously described in detail (GUSTAFSSON, 1941). »In 1939 regarded as an earliness mutation.»

Straw-stiffness mutation 1 (1939: 5: 26). Discovered in the X_3 generation (1939). Plant sterility = 59 %. Arose in the same series as the preceding mutation. An *albina* mutation occurred simultaneously. »Stiffer straw, shorter.»

Straw-stiffness mutation 2 (1939: 6: 3). Discovered in the X_3 generation (1939). 630 seeds, desiccated above concentrated H_2SO_4 and irradiated, gave rise to 46 full-grown plants (= 7 %), 17 of which

were completely sterile. The immediate germination was 16 %. By laboratory cultures of the X_3 generation 31 % chlorophyll mutations arose. In the same series a vital mutation having a somewhat lighter green colour than Golden barley was obtained. »Stiffer and shorter straw. Ears broad and erect.»

The last three mutations were detected in 1939. It is evident that no pronounced selection could be carried out in the short time available. Possibly semilethals or minor deleterious mutations still influence the production. Completely fertile individuals, however, served as mother plants for the yield trial, the same thing naturally also being true of the previous mutations. One of the new mutations, straw-stiffness mutation 1 (1939: 5: 26), was attacked by open smut, its yield probably being lowered somewhat on that account.

The yield experiment was carried out in the following manner. Of 50 small field-plots 6 contained Maja barley, 4 Golden barley and 10×4 the mutations. Each plot measured 75×300 cm. and was surrounded by winter rye (45 cm.) in order to prevent border effect. In each plot 600 seeds were sown, 2 seeds into every hole (dense stand) and 5×60 holes. The series were repeated four times: I was given a fertilization of 200 kg. nitrate of lime per hectare, II a fertilization of 300 kg. per hectare, III a fertilization of 400 kg. per hectare, and IV (= I) a fertilization of 200 kg. per hectare. The order of the strains and mutations was:

	I	II	III	IV
Maja barley	1 a, 6	18	30	42, 47 a
Golden barley	7	19	31	43
Erectoides 1	1	13	25	37
Erectoides 2	2	14	26	38
Erectoides 3	3	15	27	39
Erectoides 4	4	16	28	40
Erectoides 5	5	17	29	41
Lemma-like glumes ...	8	20	32	44
Late mutation	9	21	33	45
Leaf colour mutation ..	10	22	34	45 a
Straw-stiffness mut. 1..	11	23	35	46
Straw-stiffness mut. 2..	12	24	36	47

The sowing took place on May 3rd. Favourable weather at the time forced the seeds to almost immediate and fairly good germination. Differences in germination rate and sprouting capacity were conspicuous.

Erectoides 4 and 5, for instance, germinated more slowly than the other erectoides types, and during the first weeks the seedlings of erectoides 4 appeared to be weak. Particularly fast-germinating and rapid-growing in the beginning was 1939: 14: 32 (lemma-like glumes). Its lowered production in comparison to Golden barley therefore depends probably less on an constitutional weakness than on some ear or flower abnormality (note the transformed glumes!), or on a decreased tillering.

Weather conditions in the summer months of 1940 differed greatly from the normal (see the data below on precipitation, number of sun hours and mean temperature of May, June, July and August 1940 in comparison with the corresponding averages of 1920—1939). May and especially June were abnormally dry, which lessened the influence of fertilization for all summer crops. But owing to a fall of no less than 7 mm. rain on May 6th—8th, the seedlings of the present yield experiment got an especially good start. In the beginning of August heavy and continuous rains prevented and delayed harvest and probably decreased the quality in some respects.

Weather conditions in 1920—1939 and 1940 at Svalöf.

	Precipitation (mm.)		Number of sun hours		Mean temperature (°C.)	
	1920—1939	1940	1920—1939	1940	1920—1939	1940
May ..	50,6	25,6	233,9	284,5	+ 10,7	+ 11,3
June..	59,7	8,6	229,1	365,0	+ 13,8	+ 16,9
July ..	90,4	91,2	224,9	221,5	+ 16,6	+ 16,6
August	88,0	89,0	202,7	170,5	+ 15,8	+ 14,2

Most of the mutations set ears at about the same time as Golden barley (June 27th) or one—two days later. Maja barley was evidently delayed (June 29—30th). The late mutation (1939: 13: 65) and erectoides 3 (1939: 14: 1) were up to 5—6 days later. The time of ripening was approximately identical for most of the mutations and for Golden barley and Maja. The straw-stiffness mutation 1 (1939: 5: 26) and erectoides 1 were one or perhaps two days earlier. The late mutation (1939: 13: 65) and erectoides 3 (1939: 14: 1) were rather late in ripening (4—7 days). The leaf colour mutation (1939: 5: 9), which was regarded as an earliness mutation in 1939, ripened 4—5 days later than Golden barley. Owing to the unusual weather conditions in 1940 these data are probably of little value. In regard to other characters as straw-stiffness even the morphological mutations displayed great differences. Especially stiff was erectoides 2, less so erectoides 5 and 4. Erectoides 3

lodged somewhat after the heavy rains in July, in spite of its considerable straw-thickness, but less than Golden barley itself.

Yield results. — In Table 1 a survey of the four series is given. The totals of series I—IV, and from that the differences from Golden barley (in per cent), are calculated for each variety. All weights are in grams.

Most of the mutations (7 out of 10) decrease the production as

TABLE 1. *Comparative yield-trial of ten mutations in barley produced by X-ray irradiation.*

Name	No.	Series I	Series II	Series III	Series IV	I—IV	Difference from Golden barley
Erectoides 3.....	1939:14: 1	1060 gr.	1120 gr.	1220 gr.	1080 gr.	4480 gr.	+ 11,72 %
Maja barley	*1939: 5*	*1135* » [1]	*1070* »	*1130* »	*1095* » [1]	*4430* »	+ *10,47 %*
Late mutation...	1939:13:65	1050 »	1150 »	990 »	1150 »	4340 »	+ 8,23 %
Erectoides 1.....	1939:13:22	1100 »	930 »	1090 »	940 »	4060 »	+ 1,25 %
Golden barley ...	*1939:14: 2*	*900* »	*1070* »	*1040* »	*1000* »	*4010* »	—
Leaf-colour mutation	1939: 5: 9	840 »	1020 »	870 »	930 »	3660 »	— 8,73 %
Erectoides 2.....	1939:13:38	1040 »	750 »	920 »	810 »	3520 »	— 12,22 %
Erectoides 5.....	1939:14:20	870 »	840 »	850 »	770 »	3330 »	— 16,96 %
Erectoides 4.....	1939:14: 9	800 »	950 »	700 »	780 »	3230 »	— 19,45 %
Straw-stiffness mut. 2.....	1939: 6: 3	650 »	840 »	730 »	820 »	3040 »	— 24,19 %
Lemma-like glumes	1939:14:32	830 »	700 »	700 »	750 »	2980 »	— 25,69 %
Straw-stiffness mut. 1.....	1939: 5:26	810 »	760 »	640 »	710 »	2920 »	— 27,18 %

measured in comparison with Golden barley, three of them not less than 25 %. The two straw-stiffness mutations included in the experiment are valueless from a practical point of view. The same thing is true of four morphological mutations, especially of 1939: 14: 32 (lemma-like glumes), in spite of its considerable interest to morphology. The leaf colour mutation, which in a certain sense can be regarded as a chlorophyll mutation (turns yellowish at the time of earing), is remarkably good (a decrease of 9 %). In no series does any of these

[1] The mean of two yield plots.

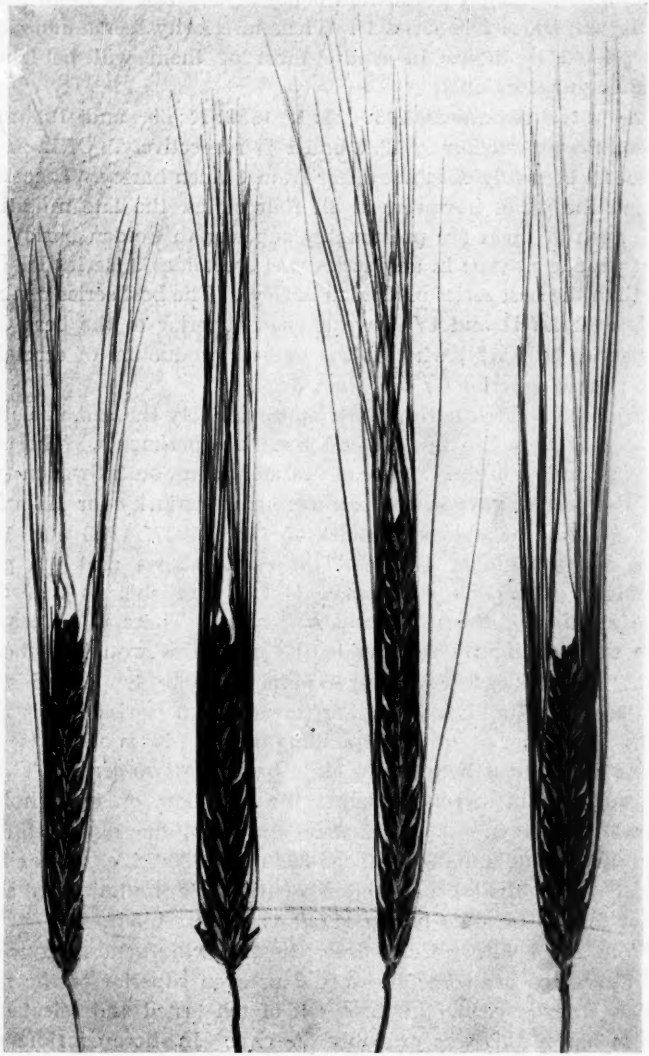

Fig. 1. Three vital mutations of practical interest. From left to right: Golden barley, erectoides 1, late mutation and erectoides 3. — Photo H. OLSSON, Svalöf.

seven mutations give a production equal or superior to Golden barley (save for erectoides 2 in series I). Their inferiority seems undoubtedly to be proved by now. In future most of them will be kept for theoretical purposes only.

The three mutations 1939: 14: 1, 1939: 13: 65, and 1939: 13: 22 increased the production by 12, 8 and 1 % respectively. Of these types erectoides 1 probably does not differ from Golden barley. Erectoides 3 increased the yield, however, in all four series, the late mutation in three. Both of them are presumably superior to Golden barley. The highest producing type in any series was erectoides 3, series III (14 % better than the best series of Golden barley). The best series of the late mutation (series II and IV) gave a yield superior to the best Golden barley series by 7,5 %, whereas the highest production of erectoides 1 (series I) was superior by less than 3 %.

Maja and Golden barley show approximately the same relation in yield as that found in the original Danish experiments. The official yield experiments in the County of Malmöhus in South Sweden (where Svalöf is situated) gave in 1939 an average superiority for Maja barley of 14 %, and the average results of 1936, 1937, 1938 and 1939 a corresponding value of 12 %. This result shows that the present preliminary production experiment is fairly reliable as regards the mutual relation of the two standard strains. There is no reason to believe that the figures relating to the mutations would be more erroneous. Erectoides 3 is superior to Maja barley by 1,25 % and is better in two series. The highest value of erectoides 3 (series III) is no less than 7,5 % superior to the corresponding figure of Maja barley (series I). The late mutation is better than Maja barley in two series. The very low production in series III makes the mutation, on the whole, unfavourable to Maja. If we exclude series III, the figures for Maja barley and for the mutation will be 3350 and 3300, i. e. approximately identical. The highest production of the late mutation is slightly superior to that of Maja barley (1150 as against 1135).

From these data we can draw the following general conclusion: X-ray mutations are sometimes equal or even superior to the mother strain as regards yield. In three out of ten tested and selected mutations in barley this was probably the case. In these expriments two mutations are not only superior to the mother strain but equal (or in one case possibly slightly superior) to the highest-yielding barley variety cultivated in Scandinavia. As yield is the outcome of a series

of physiological properties, the high-yielding mutations, at least from the plant-breeder's point of view, must be regarded as progressive.

A further study will immediately reveal one of the main reasons for the different yield results (Table 2). The 1000-grain weight is essentially higher in erectoides 3 and the late mutation (as well as in Maja barley) than in the original strain (58,2 and 53,4 as against 50,9). An easy calculation demonstrates that the superiority of erectoides 3 is

TABLE 2. *Chemico-physiological properties of ten mutations in barley.*

Name	No.	1000-grain weight	Protein content [1]	Starch [2]	Sifting through three different sieves			
					I (2,5 mm.)	II (2,5 mm.)	III (2,2 mm.)	IV
Erectoides 3 ...	1939 : 14 : 1	58,2 gr.	11,48 %	60,40 %	90,2 %	8,1 %	1,2 %	0,4 %
Maja barley ...	*1939 : 5*	*55,2 »*	*11,97 %*	*59,03 %*	*86,6 %*	*10,8 %*	*1,8 %*	*0,9 %*
Late mutation	1939 : 13 : 65	53,4 »	12,30 %	59,53 %	86,4 %	12,4 %	0,9 %	0,3 %
Erectoides 1 ...	1939 : 13 : 22	50,0 »	13,80 %	56,75 %	78,7 %	18,5 %	2,3 %	0,6 %
Golden barley..	*1939 : 14 : 2*	*50,9 »*	*13,80 %*	*57,80 %*	*86,1 %*	*11,8 %*	*1,8 %*	*0,4 %*
Leaf-colour mutation.....	1939 : 5 : 9	45,4 »	14,65 %	56,68 %	54,9 %	39,8 %	4,1 %	1,2 %
Erectoides 2 ...	1939 : 13 : 38	49,5 »	14,58 %	55,40 %	83,2 %	14,3 %	2,1 %	0,5 %
Erectoides 5 ...	1939 : 14 : 20	46,5 »	14,95 %	54,98 %	71,8 %	23,9 %	2,9 %	1,4 %
Erectoides 4 ...	1939 : 14 : 9	46,9 »	15,15 %	54,58 %	69,2 %	26,3 %	3,2 %	1,4 %
Straw-stiffness mut. 2.....	1939 : 6 : 3	49,1 »	14,28 %	56,80 %	77,0 %	18,0 %	4,0 %	1,0 %
Lemma-like glumes.....	1939 : 14 : 32	51,3 »	15,65 %	56,53 %	87,3 %	11,6 %	1,0 %	0,2 %
Straw-stiffness mut. 1	1939 : 5 : 26	45,2 »	16,03 %	56,35 %	29,3 %	58,9 %	10,1 %	1,7 %

in fact due to the increased size and weight of the kernels. The inferior mutations — with the exception of the one with lemma-like glumes — had a distinct decrease of kernel weight. This is especially true of the leaf colour and one straw-stiffness mutation (1939 : 5 : 9 and 1939 : 5 : 26). The low production of the last-mentioned mutation is probably due to a great extent to this property. More remarkable is the fairly high production of the leaf colour mutation despite the small kernels. If we calculate the number of seeds produced in the six best members of the yield table, we shall find a total production of 81300 kernels in the late mutation, 81200 in erectoides 1, 80600 in the leaf

[1] Rude protein (nitrogen × 6,25) in % of the dry substance.

[2] In % of the dry substance.

colour mutation, 80300 in Maja barley, 78800 in Golden barley, and 77000 in erectoides 3. Thus, as pointed out above, the higher yield of erectoides 3 is exclusively due to the very high 1000-grain weight. The late mutation does not only possess a higher 1000-grain weight but also a much more pronounced seed production. With regard to the latter property it is even superior to Maja barley. Also the leaf colour mutation is superior in this respect to both standard strains. Therefore this mutation is not entirely without practical interest.

Columns 6—9 give the results after siftings through three sieves of different widths. The last percentage illustrates the amount of kernels useless for malting purposes. It will at once be seen that the three best mutations have the same quality in this respect as Golden barley and are somewhat superior to Maja barley. The inferior mutations — even here with the exception of the lemma-like glume mutation — have much higher percentages of rubbish, this being especially true of the straw-stiffness mutation 1, where the largest sieve (I) does not hold more than 29 % of all kernels against 90 % for erectoides 3 and 86 % for Golden barley.

It would appear as if the 1000-grain weights are unusually high in these yield experiments. The official data for 1939 (County of Malmöhus) gave the 1000-grain weights as 38,0 for Golden barley, 40,2 for Kenia, 39,6 for Maja, 40,4 for Opal B, and 39,9 for the Svalöf strain 30/19. In the extensive yield experiments at Svalöf Barley Department from 1940 Kenia barley had, however, a 1000-grain weight of 50,0, Maja barley a weight of 52,0, and Opal B a weight of 53,0, i. e. these figures are just a little below those of the writer's experiments.

We can conclude from this survey that by mutating Golden barley might be changed into a plus as well as into a minus direction in regard to kernel size and kernel number. In most cases the two plus-properties exclude each other (erectoides 3, erectoides 1, the leaf colour and the glume mutation) but in one case they are united (the late mutation). The minus-properties are, however, easily combined.

The protein and starch contents vary widely. We find a pronounced negative correlation betwen yield and protein content, but this is probably due partly to differences in the density of the stands. An interesting feature, however, is that erectoides 3 with a fairly low kernel production has a high starch and a low protein content. Since this mutation is characterized by very thick stems and unusually broad leaves, the density also in this case probably influences the chemical properties. Progeny tests for several years will be required in order to prove whether

hereditary changes, partially independent of exterior conditions as density and climate, have here an effect on the protein content.

Of considerable interest are the data on germination ripeness (Table 3). This property is very important, especially for malting and brewing purposes. Golden barley has a short period of decreased germination. Already in one or two months it is capable of almost full germination (October 9th, 1940: 94 %), but this quality is not complete until the beginning of November (November 9th: 98 %). Maja

TABLE 3. *Germination ripeness.*

Name	No.	Germination on Nov. 9th, 1940	Germination on Oct. 9th, 1940	Difference	D/m
		Morphological mutations			
Lemma-like glumes	1939 : 14 : 32	97,88 % ± 0,51 %	95,88 % ± 0,70 %	2,00 % ± 0,86 %	2,33
Erectoides 1...	1939 : 13 : 22	97,64 % ± 0,54 %	93,50 % ± 0,87 %	4,14 % ± 1,02 %	4,05
Golden barley	*1939 : 14 : 2*	*98,38 % ± 0,45 %*	*93,88 % ± 0,85 %*	*4,50 % ± 0,96 %*	*4,69*
Erectoides 2...	1939 : 13 : 38	97,75 % ± 0,52 %	91,75 % ± 0,97 ±	6,00 % ± 1,10 %	5,45
Erectoides 5...	1939 : 14 : 20	96,63 % ± 0,64 %	88,88 % ± 1,11 %	7,75 % ± 1,28 %	6,05
Erectoides 4...	1939 : 14 : 9	97,40 % ± 0,56 %	87,25 % ± 1,18 %	10,15 % ± 1,31 %	7,75
Erectoides 3...	1939 : 14 : 1	92,38 % ± 0,94 %	73,50 % ± 1,56 %	18,88 % ± 1,82 %	10,37
		Physiological mutations			
Straw stiffness mut. 1	1939 : 5 : 26	96,38 % ± 0,66 %	95,38 % ± 0,74 %	1,00 % ± 0,99 %	1,01
Leaf-colour mut.	1939 : 5 : 9	95,38 % ± 0,74 %	94,00 % ± 0,84 %	1,38 % ± 1,12 %	1,23
Late mutation	1939 : 13 : 65	97,50 % ± 0,55 %	92,88 % ± 0,91 %	4,62 % ± 1,06 %	4,35
Golden barley	*1939 : 14 : 2*	*98,38 % ± 0,45 %*	*93,88 % ± 0,85 %*	*4,50 % ± 0,96 %*	*4,69*
Straw-stiffness mut. 2	1939 : 6 : 3	97,25 % ± 0,58 %	87,75 % ± 1,16 %	9,50 % ± 1,29 %	7,36
Maja barley ...	*1939 : 5*	*98,67 % ± 0,33 %*	*90,33 % ± 0,85 %*	*8,34 % ± 0,91 %*	*9,16*

barley has a somewhat slower rate of germination ripening (°/10 1940: 90 % as against 99 % on °/11 1940). The difference between Maja and Golden barley is statistically significant (D/m nearly equal to 3).

The mutations differ strikingly between themselves. The data for Golden barley are used as standard figures. Here we find a difference in germination between November and October of 4,5 % ± 0,96 %, D/m = 4,69. The mutations may be divided into two groups, comprising either morphological or physiological types. Maja barley will also be placed in the latter group. In the first group two mutations have decreased the difference between November and October data, and this

is especially true of the mutation with lemma-like glumes. The difference between November and October germination is probably still significant (D/m = 2,33), but it is nevertheless distinctly lower than that of Golden barley (D/m = 4,69). Erectoides 1 behaves approximately like Golden barley (D/m = 4,05 against 4,69). Four erectoides types decrease the rate of germination ripening, in three cases quite considerably (D/m for the difference between erectoides 5 and Golden barley greater than 2), and in the case of erectoides 4 and 3 the D/m:s are even greater than 3. It is surprising that four out of five mutations possessing the erectoides character retard the germination ripening. The data are not sufficient to prove, however, that this physiological change is frequently for some unknown reason due to the morphological character of ear density itself, but it is certainly suggestive that the most extreme mutation (erectoides 3, equal to true *erectum* types in regard to kernel characters) exhibits the greatest difference. In fact, even on Nov. 9th it had not acquired a full germination ripeness (92 %).

In the physiological group two mutations (straw-stiffness mutation 1 and the leaf colour mutation) increase the germination rate so much that no significant differences are found between the November and October figures, i. e. the differences are even smaller than that of the glume mutation in the morphological group. They differ significantly from Golden barley. The late mutation behaves approximately like the mother strain. No physiological mutation gives such a difference between November and October data as Maja barley, but straw-stiffness mutation 2 is nevertheless significantly different from Golden barley (9,50 % ± 1,29 % as against 4,50 % ± 0,96 %). Of four mutations in the physiological group two or three increase and one decreases the rate of kernel ripeness.

By these last studies it has been definitely proved that (apart from kernel weight and kernel production) mutations altered the properties of Golden barley in plus or in minus direction also in regard to physiological properties as, for instance, germination ripeness. High-yielding varieties displaying qualities, inferior from some physiological point of view, might in future be improved by the simple expedient of X-radiation and a subsequent strong selection.

Finally, it must be pointed out that erectoides 1, which differs greatly from Golden barley in morphological respects (except for the number of barbs on the side nerves of the seeds, erectoides 1 having 3,15 barbs per nerve against 4,45 for Golden barley), is very similar to Golden barley in all examined chemico-physiological properties. Its

yield is approximately identical (4060 against 4010 grams). The same thing is true of the 1000-grain weight (50,0 against 50,9), of nitrogen content (13,80 % against 13,80 %), of starch content (56,75 % against 57,80 %), of useless kernels (0,6 % against 0,4 %) and, finally, of germination ripeness (D/m = 4,05 against 4,69 for Golden barley).

Once more the present writer wishes to point out that one year's yield experiments are not sufficient to define the exact relative production of a mutation. But the data should be reliable enough *to prove the superiority of some mutations in relation to the mother type.*

MUTATIONS AND EVOLUTION.

What does a vital mutation, a progressive variation really imply? A distinction must at once be made, differing somewhat from the usual reasoning. A newly arisen mutation need not necessarily excel the original biotype or population in order to be regarded as progressive or have an evolutionary value. The significance of a mutation is not determined by its rate of development, its fertility or its power of competition under unchanged conditions, but the criterion of its value is instead: *Does any environment exist, extreme or not extreme, where the mutation in question is able to hold its own or surpass the mother type?* Recent studies on the problems of polyploidy have proved for certain that many coenospecies (TURESSON) comprise chromosome races (cytological ecospecies) arisen after a doubling of ± identical genomes. They are said to be autogenomatic or autopolyploid. These autopolyploids have frequently a distribution area separated from that of the diploid (MÜNTZING, 1936, and later authors). Within the range of the diploid they cannot compete or even occur. Their ecology, physiology and consequently their distribution will be affected. They break the ecological possibilities of the diploid.

The same reasoning should be valid of mutations, whether they consist of rearrangements or of intragenic changes.

Under unchanged conditions most spontaneous or induced mutations decrease the vitality. Rather commonly this decrease in vitality is noticeable already in a heterozygous state. This has been proved, for instance, with respect to the gene singed in *Drosophila funebris* (TIMOFÉEFF-RESSOVSKY, 1934).

Even the recessive factors *y* and *w* in the X-chromosome in *Drosophila melanogaster* are inferior to the wild type. But in cultures exposed to high temperatures (36° C. or more) *w*(*yw*)-flies are rather resistant to the heat, more so than the original stock. To cite HERIBERT

NILSSON (1931), who was the first to show this fact: The single interpretation, which can be presented in order to explain these very consistent results, is that the mutation type *w*(*yw*) has a better vitality at the induced critical temperature than the wild type. — According to the same author (1932), this state of things applies even to the Bar-mutation, with the difference, however, that the high temperature is not the extreme environment but the food substratum. In old, decaying cultures Bar showed an increased vitality compared with the wild type. Instead of 36 % of all flies in a mixed population under normal conditions it constituted 69 % in cultures with a decomposed substratum.

Similar results have been published by other scientists. A few examples will suffice. Already in 1928, BANTA and WOOD described their well-known heat race of *Daphnia longispina*. Normal *Daphnia*-animals live in water having a temperature between 12° and 26° C., the optimum lying at 17°—21° C. From this 20°-population a heat race arose by mutation having an optimum of 25°—28° and a temperature range of 21°—32°. If a sudden change of temperature happened in such a *Daphnia*-pond, so that the temperature rose to 28°—30°, all normal animals would disappear, and just those variations would be left, which by mutation- and combination-processes had altered their temperature range previously. A mutation hardly viable under normal conditions may surpass the mother type in an extreme environment.

Some years ago TIMOFÉEFF-RESSOVSKY (1934) made an elaborate study of six spontaneous and induced mutations in *Drosophila funebris*. Under normal culture conditions the factor eversae (*ev*) had a slightly higher relative vitality than the standard stock, the other five mutations showed a more or less decreased viability. Some varying culture methods were tried (population density and temperature). The experiments showed that eversae was superior only at a low or normal population density, but decreased in vitality when the culture glasses were overcrowded. The dominant factor venae abnormes, which had a relative ♂ vitality of 4,8 % and a relative ♀ vitality of 88,9 % (as a heterozygote), showed an almost normal ♀ vitality in underpopulated cultures. Similarly, at a temperature of 24°—25° C. eversae was more vital than the mother stock, but slightly inferior at very low and at very high temperatures. The relative vitality of venae abnormes increased at low temperatures, that of bobbed at high temperatures. None of these mutations — although situated in the same chromosome — presented an identical norm of reaction.

Recently KÜHN and ENGELHARDT (1937) made an investigation

concerning the relative vitality in different environments of a melanistic mutation in *Ptychopoda seriata*. The mutation is inferior to the mother type under normal conditions but superior at a low temperature and a high humidity.

These few cases are sufficient to prove that, like autopolyploids, even seemingly inferior mutations frequently widen the variation of a species or variety, break its frame-work and produce new ecological and physiological possibilities. As emphasized already by TIMOFÉEFF-RESSOVSKY (1934, p. 339), most mutations exhibit probably a specific mode of reaction to exterior conditions. The normally inferior ones are due when their individual properties can act at extreme changes in environment. Mutations, showing a decreased vitality under normal conditions, may have an evolutionary significance.

These results make the logical position of the anti-mutationists unfavourable. The failure of their standpoint, however, would be incomplete if cases of increased vitality even at normal or unchanged conditions were unknown.

In his investigation from 1923, GONZALEZ showed that certain II-chromosome mutations in *Drosophila melanogaster* increased the duration of life (black and speck) in contrast to others which decreased it (purple, vestigial, arc). The duration of life is certainly not equal to vitality but ought to be one of its components. It was for wild flies 39,5 days, for black 40,7, for speck 42,7, for purple, vestigial and arc 24,5, 18,2 and 26,8 days respectively. If these factors are combined, they will give very different results. The double recessive of purple and arc has a longevity of 33,7 days, i. e. it lives longer than both its components. Purple—arc—speck has a longevity of 39,6 days, i. e. in spite of the two inferior genes purple and arc it equals the wild type. The recessive factor speck counteracts the effect of the two deleterious genes. These experiments prove that some mutations increase vitality even under normal conditions, and that the effect of individual genes depends on the remaining genotype. Two or more inferior factors may counterbalance each other. In 1934 TIMOFÉEFF-RESSOVSKY made similar experiments with *Dr. funebris*, showing the importance of genic cooperation and genotypic environment to the relative vitality of a mutation.

DOBZHANSKY and QUEAL (1938) examined the genic variability of different natural populations in *Drosophila pseudoobscura*. 3,5 % of all III-chromosomes contained recessive visibles. The number of lethals and semi-lethals amounted to about 15 %, and the number of minor deleterious variations to about 39 %, making in all more than 50 %.

Furthermore, the authors proved that at least some lethals were incompletely recessive. In addition to these detrimental mutations they found about 2 % of all examined III-chromosomes carrying factors increasing viability above the average. This study forms a valuable complement to the more pronounced laboratory researches of GONZALEZ and TIMOFÉEFF-RESSOVSKY.

As already mentioned, TIMOFÉEFF-RESSOVSKY (1935) was the first to discover the existence of induced mutations increasing the relative vitality (see p. 341). In this paper some more data have been accumulated. Certainly we know nothing about the vitality of the favourable barley mutations under wild conditions, but then we cannot even suppose that Golden barley itself would be competitive in nature. The yield capacity of the mother strain is surpassed. This cannot in any case imply that in the culture conditions prevailing (normal environment) the mutations are less vital than the original strain.

To sum up: Mutations are found in nature and in experiments, displaying equality or superiority to the mother type even under unchanged (= normal) conditions. Unfavourable mutations exert their negative effect on vitality under normal conditions. When the exterior conditions are changed, these mutations may, however, turn out as favourable. Save for their decrease in vitality, most visibles have a specific mode of reaction to environment. To denote them as absolutely and once for all inferior would imply that experiments could cover all environmental possibilities. Inferior as well as vital mutations form ingredients for nature's reiterated attack on the existing appearance and structure of species and genera. The inferiority of mutations in nature is counteracted, either by a changed environment, where the normal type cannot compete, or by a combination with modifying genes and rearrangements. According to this explanation, visibles themselves are active not only as regards the morphological but also the physiological differentiation of populations.

This discussion has stressed the similarity of autopolyploids and mutations as to ecological and physiological possibilities. It is the writer's opinion that no theory on natural selection and dominance can avoid taking the ecology of the gene into consideration.

PLANT-BREEDING AND MUTATIONS.

In the same manner as many visible mutations have their own mode of reaction to environmental changes, there is a possibility that

they have a specific mode of origin, corresponding to differences in the underlying chemical structure. Principally an intentional direction of the mutation process could be carried out in such a case. STADLER and co-workers (1936, 1937) separated the structural chromosomal changes from each other. Translocations arise primarily after bombardments with rays of short wave-lengths, but deficiencies appear as well in ultraviolet regions, the rays having longer wave-lengths. Position effects due to chromosomal rearrangements (although not detected so far in *Zea mays*) cannot thus arise in ultraviolet.

Another way of approaching the same problem was shown in a paper by the present writer (GUSTAFSSON, 1940). Chlorophyll mutations belonging to different phenotypic groups (*albina*, *xantha*, *viridis*, etc.) respond to X-ray dose, chromosomal disturbances, cell environment at the time of irradiation in a specific way, the mutation process being in a certain sense open to an intentional regulation. *Alboxantha* mutations, for instance, cannot arise, or do so very infrequently, after an irradiation of dry cell nuclei. A further result of interest is that the different mutation groups behave as units. Whether this indicates that individual mutations in a group originate in genes or groups of genes having a similar basic structure, is impossible to say as yet.

Most mutations appear to be inferior in comparison with the mother type. This is probably due in many cases to a disturbed balance between mutation and genic environment. As already pointed out, this destroyed cooperation may be counteracted by structural rearrangements. Obviously these will frequently combine with deficiencies and lethals in irradiation experiments, but sometimes they show no detrimental features, making the intragenic mutation part of a congruous entirety. In such a case a progressive, favourable variation will arise. In future plant-breeding will have to remodel genomes and remake genes, building up hundreds or thousands of new harmonious genotypes.

SUMMARY.

1. At the Svalöf Seed Association yield experiments have been carried out with ten induced mutations in barley, their mother strain Golden barley, and the highest-yielding variety cultivated in Scandinavia, Maja barley.

2. Seven out of ten mutations decreased yield considerably (from 9 to 27 %), but three equalled or surpassed the mother strain. One (or maybe two) attained the level of Maja barley.

3. The 1000-grain weight can be changed in both directions, three mutations increasing and seven decreasing kernel size and weight. The number of ripe kernels produced by the different mutations can be either higher or lower than in Golden barley itself. In one case (a late mutation, 1939: 13: 65) a higher weight is combined with a greater kernel number, in four cases (erectoides 3, erectoides 1, a leaf colour, and a glume mutation) these two properties exclude each other. The negative properties (low kernel weight and number) are combined in five cases.

4. Protein and starch contents have been examined. There is a pronounced negative correlation between yield and protein content.

5. Germination ripeness is easily changed. Mutations have been found, which increase the immediate germination up to about 100 %, as well as mutations decreasing the rate of germination ripening considerably.

6. Some general problems concerning the significance of mutations to evolution are discussed. A general definition of the term »progressive mutation» has been attempted.

7. Future tasks of plant-breeding in regard to irradiation problems and induced mutations are formulated.

These and previous mutation experiments have in part been carried out at the Svalöf Seed Association, in part at the Institute of Genetics, Lund University. The writer is indebted to the late head of these two Institutes, Prof. Dr. H. NILSSON-EHLE, for valuable advice and discussions, as well as to the present heads, Prof. Dr. Å. ÅKERMAN and Prof. Dr. A. MÜNTZING. Financial assistance has been generously given by A.-B. Saltsjöqvarn, Stockholm.

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KEIMUNG UND TRIEBKRAFT BEI HAFER UND WEIZEN NACH VERSCHIEDENEN RÖNTGENDOSEN

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(With a Summary in English)

EINLEITUNG.

IN der heutigen Mutationsforschung spielt Röntgenbestrahlung als Mittel zum Hervorrufen induzierter Mutationen eine weitaus überragende Rolle. Die verschiedensten Organismen werden X-Strahlen variierender Wellenlänge exponiert und die gröberen oder feineren Änderungen der Genome dann untersucht. Unter erfolgreich bearbeiteten Pflanzen sei nur beispielsweise an *Zea*, *Antirrhinum* und *Hordeum* erinnert. Bei der letzten Getreideart ist in Schweden in den letzten Jahren von GUSTAFSSON eine Reihe Untersuchungen veröffentlicht worden, die sich denen von NILSSON-EHLE anschliessen. Die Gerste ist bekanntlich ein zu Mutationsuntersuchungen gut geeignetes Objekt. Schon die Zahl spontan aufgetretener, verschiedenartiger Mutationen ist beträchtlich; durch X-Strahlenbehandlung ist sie in vielen Fällen gewaltig erhöht worden. So sind bei der Gerste zurzeit rund 900 Chlorophyllmutationen durch Röntgenbestrahlung erhalten (GUSTAFSSON, 1938, 1940). Die Frequenz der verschiedenen Mutationen kann im Vergleich mit der Frequenz in der Natur bis auf das rund 5000-fache gesteigert werden.

Bei Hafer und Weizen liegen im Vergleich mit der Gerste andere Verhältnisse vor. Bezüglich z. B. Chlorophyllmutationen sind Spontanmutationen sowie induzierte Mutationen nur äusserst selten beobachtet worden, noch seltener zu genetischer Analyse gekommen. ÅKERMAN, der im Laufe der letzten 25 Jahre als Leiter der Weizen- und Haferabteilung des Saatzuchtvereins ein ausserordentlich umfangreiches Hafermaterial in Svalöf beobachtet hat, fand während dieser Zeit nur eine, sicher spontane Chlorophyllmutation, f. *chlorina* (ÅKERMAN und FRÖIER, 1941). Es gibt indessen auch beim Hafer Mutationen, die in erheblicher Frequenz auftreten, vor allem bezüglich der Kornfarbe: in der Richtung schwarz zu weiss oder grau. NILSSON-EHLE und nachher ÅKERMAN haben feststellen können. dass die Mutationsfrequenz in einfaktorigen

Schwarzhafersorten, z. B. Svalöfs Engelbrektshafer II, in der Richtung schwarz- zu weisskörnig 1 : 2000 oder 0,5 pro mille betragen kann, was als eine auch im Vergleich mit der Gerste sehr hohe spontane Mutationsfrequenz betrachtet werden muss. Auch der verhältnismässig leicht durch Mutation auftretende Fatuoidkomplex beim gewöhnlichen Hafer muss in diesem Zusammenhang erwähnt werden.

STADLER (1929) erhielt bei Hafer und Weizen einige röntgeninduzierte Mutationen; er verglich die Resultate von Bestrahlungen einerseits von di-, tetra- und hexaploidem Hafer und Weizen, andererseits von gewöhnlicher, diploider Gerste. Es zeigte sich, dass die Mutationsfrequenz bei den diploiden Arten am grössten war. Von den Tetraploiden erhielt er nur beim Weizen induzierte Mutanten in sehr geringer Frequenz. Bei tetraploidem Hafer und hexaploidem Hafer und Weizen wurden keine Mutationen gefunden. Der Vergleich mit der Gerste ergab, dass dieselben Röntgendosen, die bei Gerste 40—70 Mutationen hätten erzeugen können, bei tetraploidem Hafer und hexaploidem Hafer und Weizen ganz ohne Wirkung blieben. STADLER fasste das infolge der Polyploidie wahrscheinlich sehr häufige Vorkommen reduplizierter Gene als generelle Ursache dieser Befunde auf. Das Auftreten dominanter Mutationen sollte durch die Polyploidie nicht vermindert werden, dagegen sehr stark das Auftreten von rezessiven Mutanten, was auch in seinem obenerwähnten Versuch der Fall war. Die Verschiedenheiten zwischen dem Mutieren bei Gerste einerseits und Hafer und Weizen andererseits sind indessen mit diesen Untersuchungen kaum erledigt und erklärt worden, und es besteht — mit Rücksicht auf eben die Gene, die nicht reduplizierten sind — wenigstens Ursache zu vermuten, dass man bei einem grösseren Material und geeigneten Röntgendosierungen sichtbare Mutationsvorgänge auch bei den Hexaploiden hervorrufen kann. Beim hexaploiden Weizen sind übrigens schon einige Röntgenmutationen erhalten worden (GUSTAFSSON, unveröffentlicht).

ÅKERMAN richtete schon früh seine Aufmerksamkeit auf die sehr geringe Frequenz von Chlorophyllmutanten bei Hafer und Weizen. Bei seinen genetischen Haferuntersuchungen leitete er 1933 Versuche mit Steigerung der Mutationsfrequenz des Hafers durch Röntgenbestrahlung und Altern der Samen ein. Bezüglich der Resultate der Röntgenbehandlungen zeigte sich im Laufe der Zeit, dass diejenigen Röntgendosen, die bei der Gerste eine erhebliche Anzahl von Mutanten erzeugten, beim Hafer vollkommen versagten. Es wurde indessen bei diesen ersten Untersuchungen noch mit verhältnismässig begrenzten Röntgendosen, 10000 r nicht übersteigend, gearbeitet. Daher konnten bei der

von ÅKERMAN untersuchten diploiden *Avena strigosa* keine induzierten Mutanten beobachtet werden, obwohl man ja hier a priori leichter das Auftreten induzierter Rezessivmutanten hätte erwarten können. Sie sind früher von STADLER auch auf diesem Wege erhalten worden.

In den nächstfolgenden Jahren konnte GUSTAFSSON bei *Hordeum* zeigen, dass sowohl die Zahl verschiedener Mutationstypen als auch die Frequenz ein und desselben Typus erheblich anstieg bei so kräftigen Röntgendosen, dass die Keimfähigkeit der behandelten Körner auf 5—10—20 % gesunken war. Infolge dieser hohen Dosen traten nach seinen Untersuchungen tiefgreifende, letal wirkende Störungen der behandelten Pflanzen auf, die zu totaler oder partieller Sterilität führten, daneben auch weniger letale, die entweder zytologisch als gröbere oder feinere Chromosomenveränderungen studiert werden konnten oder auch zytologisch nicht feststellbar waren, und die sich morphologisch-genetisch durch verschiedene ausspaltende Mutanten verrieten (GUSTAFSSON, 1940).

Auf Anregung von Prof. ÅKERMAN habe ich seine früheren Röntgenbehandlungsserien mit Hafer und Weizen fortgesetzt, wobei zunächst versucht wurde, die Röntgendosen so zu erhöhen, dass die Keimfähigkeit der Körner von *Avena strigosa* bis auf etwa 5 % abnahm. Hierbei sollte sich zeigen, ob auch hier wie bei *Hordeum* die Mutationsfrequenz erheblich ansteigen würde. Die Erwartungen wurden erfüllt, indem 1940 in X_2 nach einer X_1-Generation mit nur 5 % Aufgang 1939 mehrere Chlorophyllmutanten ausspalteten, darunter drei, allem Anschein nach sehr nahe mit den von STADLER gefundenen übereinstimmend (STADLER l. c.). Auch bei *Triticum monococcum*, ebenfalls stärkerer Röntgenbehandlung ausgesetzt — bis zu 5 % Aufgang der X_1 — traten einige interessante chlorophylldefekte Mutanten auf. Da eine eingehendere genetische Analyse der gefundenen Mutanten beabsichtigt ist, werden die genannten preliminären Resultate nur auf diese Weise kurz erwähnt.

Auf Grund der erwähnten Befunde von GUSTAFSSON und meiner folgenden Beobachtungen an stark röntgenbehandeltem diploiden Hafer und Weizen wurde nun angestrebt, die Röntgenbehandlungen mit grösseren Dosen als vorher bei polyploidem Hafer und Weizen fortzusetzen. Durch eine grosszügige Donation seitens der A.-G. Saltsjöqvarn, Stockholm, an den Schwedischen Saatzuchtverein konnten die Versuche mit röntgeninduzierten Mutationen auch auf andere Pflanzenarten als Gerste erweitert werden. Die Bestrahlungen konnten nun viel weiter getrieben werden, da uns die Hilfsmittel des hochmodernen Radiophysischen Instituts, Karolinisches Krankenhaus, Stockholm, zur Verfügung ge-

stellt wurden. Dem Direktor des Radiophysischen Instituts, Herrn Dozent Dr. ROLF SIEVERT, sei hier herzlich Dank gesagt für seine Güte, die Röntgenbehandlung des Hafer- und Weizenmaterials sehr exakt ausführen zu lassen.

Bei den derart ermöglichten Bestrahlungen wurde in erster Linie darauf abgezielt, mit Körnern von annähernd normalem Wassergehalt und voller Keimreife (95—98 %) zu arbeiten, um dann festzustellen, bei welcher Röntgendosierung die Keimungshemmungen von obenerwähnter Stärke auftreten. Zwar können bei diesen Röntgenbehandlungen, wie u. a. GUSTAFSSON bei Gerste gezeigt hat, durch verschiedenen Vorbehandlungen, vor allem durch Vorquellung in Wasser, viel grössere mutationsauslösende Wirkungen bei verhältnismässig niedrigen Röntgendosen auftreten. Doch hat man dabei Bedingungen, die schwieriger konstant zu halten sind, wenn es gilt, Serien von zunehmenden Röntgendosen für nachherige Feldaussaat der Körner einwandfrei zu reproduzieren. Die Feststellung des Effektes derartiger Vorbehandlungen ist immerhin sehr wichtig; bei den hier erwähnten, ersten Untersuchungen musste er ausser Acht gelassen werden. Es galt in erster Linie, durch Vorversuche im Gewächshaus eine möglichst gute Auffassung davon zu erhalten, wieviel keimende Pflanzen aus Samenportionen verschiedener Röntgenbestrahlungen erhalten werden konnten, um dann am freien Feld nur Parallelproben derjenigen Samenportionen auszupflanzen, die in die »optimal» gehemmten Keimungsbereiche fallen. Zwar kann bei einer solchen Untersuchung nichts über den Sterilitätsgrad der Pflanzen ausgesagt werden; hierzu müssen die Pflanzen am besten ihre volle Entwicklung am Feld unter natürlichen Verhältnissen durchmachen. Parallelproben der verschiedenen Röntgendosierungen von den Körnern werden daher immer als Reserve für nachherige Kontrolle aufbewahrt.

MATERIAL UND UNTERSUCHUNG.

Als Material dieser Voruntersuchungen über die Wirkung gesteigerter Röntgendosen auf Keimung und Triebkraft diente: von *Avena sativa* die Sorte Svalöfs Siegeshafer, von *Triticum vulgare* Svalöfs Kolbensommerweizen, weiter Sommerformen von *Tr. durum*, *Tr. dicoccum* und *Tr. monococcum*. Bei der Röntgenbehandlung ging ich im Anschluss an TIMOFÉEFF-RESSOVSKY (1937) von der Auffassung aus, dass die mutationsauslösende Wirkung der X-Strahlen ihrer quantitativen Menge approximativ geradlinig proportional ist. Bei einer höheren Intensität (in r-Einheiten pro Minute ausgedrückt) kann man also kür-

zere Expositionen verwenden; bei niedrigeren Bestrahlungsintensitäten muss die Behandlung entsprechend längere Zeit dauern. Um in diesen Versuchen praktisch arbeiten zu können, wurde eine durchschnittliche Bestrahlungsintensität von 2500 r/Min. gewählt. Die Variation der Intensität innerhalb einer geschlossenen Versuchsserie war unter den herrschenden Bedingungen verschwindend klein. Zwischen verschiedenen Serien, wo die Apparatur zuweilen für andere Zwecke verwendet wurde, spielte die Variation keine Rolle, weil jedesmal neue, genaue Einstellungen der Intensität mit Ablesungen ihrer Stärke und nachfolgender Berechnung der erforderlichen Bestrahlungszeit gemacht wurden.

Die Hafer- bzw. Weizenkörner wurden in eine kleine runde, flache Papierschachtel eingeschlossen, deren Deckel und Boden je etwa 1 mm Dicke besassen. Da die Probemenge jedesmal 200 Körner betrug, bildeten diese Körner in der Schachtel zwei Schichten, nicht mehr. Bei der Bestrahlung jeder Einzelprobe wurde genau die Hälfte der berechneten Zeit von der einen Seite bestrahlt; dann wurde die Schachtel umgekippt und nun gleich lange von der anderen Seite bestrahlt. Allgemein wurde eine Rohrspannung von 176000 Volt und eine Glühstrom von 4 Milliampère Stärke benutzt. Der Fokusabstand variierte von 5 bis 6 cm; ein Kupferblechfilter, 0,05 mm dick, wurde bei allen Behandlungen verwendet. Dazu kommt noch die 1 mm dicke Pappe von Schachteldeckel und -boden. In jeder Versuchsserie ist unten die Intensität angeführt worden; dies nach den Mitteilungen von Dr. ARNE FORSSBERG, Radiophysisches Institut, Stockholm.

Von den 200 Körnern jeder Probe wurden 50 zur Keimungs- und Triebkraftsuntersuchung in kleine quadratische Kästchen gelegt. Diese Kästchen wurden mit gesiebter Erde, leichtem Ackerboden entnommen, bis 3,5 cm vom oberen Rand gefüllt; dies wird mit einem besonderen, profilierten Holzstück ausgeführt. Auf die ebene Erdfläche werden dann die Körner in regelmässigen Abständen ausgelegt. Dann wird Erde bis zum Rand aufgefüllt und abgestrichen. Alle keimenden Körner haben bei dieser einfachen Methode unter gleichförmigen Bedingungen eine Erdschicht von gleicher Tiefe zu durchdringen. Die Methode hat sich bei den Getreideuntersuchungen des Saatzuchtvereins immer gut bewährt. Nach Verlauf einer gewissen Zeit keimten zuerst die unbehandelten Körner der Kontrolle. Dann folgten stufenweise die Körner der verschiedenen Röntgenbehandlungen. Um nun hier einen Vergleich zustandezubringen, war es notwendig, die Kontrolle und die mit niedrigeren Röntgendosen behandelten Proben bis zu 15 cm oder

etwas stärker auswachsen zu lassen, bevor die wenigen Überlebenden der stärksten oder nächststärksten Röntgendosen die Erdschicht deutlich durchdrungen hatten. Es wurde dann, um die Unterschiede besser numerisch festhalten zu können, die Länge der oberirdischen Keimscheide + das erste, noch in der direkten Fortsetzung der Koleoptilenachse wachsende, nicht ganz entfaltete Blatt gemessen, nachdem es genau an der Erdfläche abgeschnitten wurde; dies geschah mit der ganzen Versuchsserie, wenn nicht mehr zu erwarten war, dass das am stärksten behandelte Glied der Serie noch mehrere Koleoptilen entwickeln würde. Als »gekeimt» wurden teils alle Körner betrachtet, die Koleoptilen durch die ganze Erdschicht treiben konnten, teils auch einige wenige, die, obwohl nicht an das Licht angelangt, doch höchstwahrscheinlich normale Keimlinge gegeben hätten, falls der Versuch lange genug hätte ausgedehnt werden können. Als »nicht keimfähige» wurden teils alle, die überhaupt keine Keimungserscheinungen zeigten (nach Abspülen der Erde), betrachtet, teils alle, die etwa Primärwurzeln, vielleicht auch ein sehr kurzes Koleoptil entwickelt haben, die aber dann in der Entwicklung offenbar stehen geblieben und eingegangen sind. Diese Aufteilung hat sich am zweckmässigsten gezeigt und ist beim Vergleich mit Auskeimungsresultaten im Dunklen bei + 12° C. auf Fliesspapier von weiteren 50 Körnern (zwecks Fixierung von Wurzelspitzen für zytologische Untersuchungen) als sehr zweckmässig befunden worden. Noch weitere 50 Körner wurden für spätere Feldversuche reserviert, und die zurückbleibenden 50 wurden in eine andere Versuchsreihe eingeschaltet, in der die kombinierte Wirkung von Röntgenstrahlen und Altern der Samen untersucht werden soll.

Bei Siegeshafer wurde die Keimung und Triebkraft in der beschriebenen Weise für die Röntgendosen 5000—60000 r untersucht, wie aus Tabelle 1 hervorgeht. Zuerst wurde eine Versuchsserie von 5000 bis 25000 r begonnen. Da indessen bei 25000 r noch 86 % Körner gut keimten, wurde eine zweite Versuchsserie mit Körnern von gleicher Herkunft und mit gleichem Wassergehalt (13 %) ausgeführt; daher das Vorkommen von zwei Kontrollen in der Tabelle. Der Zeitraum zwischen den Auskeimungen der beiden Serien war verhältnismässig gering und die Bedingungen im übrigen gleich, weshalb man die beiden Serien als gut an einander angeschlossen betrachten kann.

Bei Siegeshafer, mit einem Wassergehalt von 13 % röntgenbehandelt, traten also deutlichere Keimungshemmungen erst bei 20000 r auf; bei 40000 r konnten nur 42 % der 50 ausgelegten Körner als normal gekeimt betrachtet werden. Bei 50000 r herum war die Keimfähigkeit

Fig. 1. Siegeshafer, links unbehandelt, rechts behandelt mit 25000 r (13 % Wassergeh. der Körner, bei + 12° im Dunklen ausgekeimt, 4 Tage nach der Auslegung).

auf 26—8 % gesunken, und bei 60000 r waren alle Körner eingegangen. Auch bei dieser höchsten Bestrahlungsstärke zeigte sich jedoch beim Auskeimen auf Fliesspapier zwecks Wurzelspitzenfixierungen, dass gut die Hälfte der Körner 1—3 Primärwurzeln entwickelt hatten; einige Körner hatten auch die Koleoptilenspitze bis auf etwa fünf mm Länge austreten lassen. Nach einiger Zeit gingen indessen sämtliche derart zur Keimung gelangte Körner zugrunde. Es ist von gewissem Interesse festzustellen, dass früher auch bei Gerste deutlichere Keimungshemmungen unter ähnlichen Bedingungen erst bei 20000 r gefunden worden

TABELLE 1. *Keimungsprozente und mittlere Länge von Koleoptil + erstes, in Entwicklung begriffenes Blatt von Siegeshafer nach verschiedenen Röntgendosen. Ernte 1939, Wassergehalt der behandelten Körner 13 %.*

Zeitraum	Röntgenbestrahlung in Serie I	Röntgenbestrahlung in Serie II	% gekeimt	Mittlere Länge (mm)
Bestrahlt $^{7}/_{6}$, gelegt $^{16}/_{6}$, gemessen $^{27}/_{6}$ 1940	Unbehandelt		98	128 ± 3,2
	5000 r, 2500 r/Min		92	122 ± 3,3
	10000 r, »		92	115 ± 2,5
	15000 r, »		96	105 ± 4,0
	20000 r, »		82	89 ± 4,2
	25000 r, »		86	69 ± 4,3
Bestrahlt $^{16}/_{7}$, gelegt $^{25}/_{7}$, gemessen $^{8}/_{8}$ 1940		Unbehandelt	94	169 ± 3,6
		30000 r, 2800 r/Min	78	120 ± 4,3
		35000 r, »	66	94 ± 6,4
		40000 r, »	42	89 ± 7,4
		45000 r, »	26	88 ± 7,7
		50000 r, »	8	46 (± 10,7)
		55000 r, »	10	32 (± 8,3)
		60000 r, »	0	—

sind. CLUZET und KOFMAN fanden 1929 bei trockenen (und gequollenen) Gerstensamen bis 5000 r »schwache Förderung; erst bei 20000 r Hemmung der Keimung» (LEHMANN und AICHELE, 1931).

Ohne die erhaltenen Ergebnisse der Längenmessungen allzuviel auswerten zu versuchen, können doch diese Zahlen ein gewisses Bild von der zeitlichen Wachstumshemmung infolge der Bestrahlung geben. Obwohl, wie LEHMANN und AICHELE auch hervorheben (l. c. S. 306), die Triebkraftversuche sich über längere Perioden nach der eigentlichen Keimung erstrecken, sind sie in praktischer Beziehung für die Beurteilung der Keimung sehr wichtig und aufklärend; sie sind von mehreren

Autoren angewandt worden. Um die in Tabelle 1 erhaltenen Längenwerte vorsichtig zu deuten, kann zuerst festgestellt werden, dass eine sichere Hemmung der Zuwachsgeschwindigkeit erst bei 15000 bis 20000 r nachzuweisen ist. Bei 45000 r betrug das Längenwachstum nur die Hälfte von dem der unbehandelten Kontrolle, bei 55000 r etwa ein Fünftel. Eine nähere Betrachtung der Ursachen dieses retardierten Wachstums soll auf Grund dieser begrenzten Untersuchungen nicht angestellt werden. Es muss aber betont werden, dass man hier einen Wachstumsverlauf gemessen hat, an dem wenigstens zwei Erscheinungen beteiligt sind: teils die mehr oder weniger störend beeinflussten Kernteilungen der embryonalen Zellen, teils auch die wahrscheinlich nicht im selben Massstabe beeinflusste Streckung der letzteren, eine Tatsache, die auch z. B. bei der Untersuchung der Einwirkung von Röntgenstrahleneffekten auf keimende Pollenschläuche beachtet werden muss (cf. FRÖIER und GUSTAFSSON, 1941).

Bei Siegeshafer gelang es also festzustellen, wie weit die Röntgenbestrahlung getrieben werden musste, um die Keimfähigkeit bis auf 0 % herunterzudrücken. Damit ist laut den Verhältnissen bei der Gerste am nächsten zu erwarten, dass die Mutationsfrequenz im Bereich 45000—55000 r bei einem Wassergehalt von etwa 13 % der behandelten Karyopsen erheblich gesteigert sein soll

Bei den *Triticum*-Formen, die zur Untersuchung gelangten, wurde die Bestrahlung noch nicht so weit getrieben, dass die optimalen Bereiche herabgesetzter Keimung erreicht wurden. Immerhin sind die bisher gewonnenen Resultate in Tabelle 2 zusammengefasst worden; sie sollen später mit den Werten höherer Röntgendosen ergänzt werden. Auch di- und tetraploide Haferformen kommen später in der gleichen Art zu Untersuchung.

Wie aus Tabelle 2 ersichtlich, treten bei den hier benutzten Röntgenbestrahlungen keine so starken Keimungshemmungen wie bei Siegeshafer auf. Bei dem diploiden *Tr. monococcum* dürften wahrscheinlich erst Bestrahlungen von 20000—30000 r die erwünschten Hemmungen hervorrufen können. Bei dem tetraploiden *Tr. durum* scheinen höhere Röntgendosen als bei diploidem Weizen ohne stärkere Herabsetzung der Keimkraft vertragen zu werden. Bei *Tr. dicoccum*, ebenfalls tetraploid, wurden die Röntgendosen im Versuch nicht genügend hoch getrieben, weshalb der Vergleich hier erst nach einer zweiten, erweiterten Versuchsserie angestellt werden kann. Bei *Tr. vulgare*, *durum* und *monococcum* deuten die Triebkraftmessungen übrigens auf eine schwache Stimulation der Keimgeschwindigkeit bei 5000 r in Vergleich

zur unbehandelten Kontrolle, obwohl dies nicht statistisch sichergestellt ist. Eine ähnliche Wirkung ist auch bekannt; sie wird erklärt teils durch die Hemmung der Aktivität verschiedener Pilze (z. B. *Fusarium*) bei der Keimung, teils durch direkte Stimulationswirkung auf die Mutter-substanzen der bei der Keimung auftretenden Wuchsstoffe. Eine

TABELLE 2. *Keimungsprozente und mittlere Länge von Koleoptil + erstes, in Entwicklung begriffenes Blatt von Triticum vulgare, durum, dicoccum und monococcum, nach verschiedenen Röntgendosen. Ernte 1939, Wassergehalt der behandelten Körner 8,6—8,9 %.*

Sorte	Zeitraum	Röntgenbestrahlung	% gekeimt	Mittlere Länge (mm)
Tr. vulgare, Svalöfs Kolbensommer-weizen, 8,6 % Was-sergehalt	Bestrahlt 7/6, gelegt 18/6, ge-messen 27/6 1940	Unbehandelt	100	141 ± 6,6
		5000 r, 2500 r/Min	94	152 ± 5,7
		10000 r, »	86	121 ± 6,7
		15000 r, »	92	123 ± 5,3
		20000 r, »	78	70 ± 6,0
		25000 r, »	64	44 ± 5,5
Tr. durum, Som-merform, 8,9 % Wassergehalt	»	Unbehandelt	84	132 ± 9,0
		5000 r, 2500 r/Min	86	160 ± 6,8
		10000 r, »	76	139 ± 6,0
		15000 r, »	84	131 ± 6,4
		20000 r, »	68	79 ± 6,0
		25000 r, »	76	64 ± 7,1
Tr. dicoccum, Som-merform, 8,6 % Wassergehalt	»	Unbehandelt	100	182 ± 3,8
		5000 r, 2500 r/Min	94	184 ± 3,4
		10000 r, »	96	156 ± 4,4
		15000 r, »	100	110 ± 5,4
Tr. monococcum, Sommerform, 8,9 % Wassergehalt	»	Unbehandelt	92	131 ± 5,4
		5000 r, 2500 r/Min	96	137 ± 2,9
		10000 r, »	92	104 ± 5,0
		15000 r, »	60	59 ± 4,8

nähere Erörterung dieser noch wenig geklärten Hypothesen fällt ausser den Rahmen dieser Untersuchung.

Die weiteren Resultate der Röntgenbestrahlungen mit erhöhten Dosen sowie die von Behandlungen von diploidem und tetraploidem Hafer werden in Zusammenhang mit der genetischen Analyse aufgetretener Mutanten später veröffentlicht; das hiermit Veröffentlichte ist also als eine vorläufige Mitteilung anzusehen.

Svalöf, August 1940.

SUMMARY.

The title of the paper is: Germination and sprouting ability of oats and wheat following different X-ray dosages.

For the purpose of obtaining optimal conditions for the production of X-ray mutations in di-, tetra- and hexaploid oats and wheat, the author, induced by the results of GUSTAFSSON in his studies on barley, has determined the germination power and sprouting ability following different X-ray treatments. These varied from 5000 to 60000 r in hexaploid Victory oats, from 5000 to 25000 r in tetra- and hexaploid wheat, and, finally, from 5000 to 15000 r in diploid wheat. According to GUSTAFSSON, the highest frequency of viable and lethal mutations is obtained by X-ray dosages so heavy as to decrease the germination percentage to 5—20 %.

The dosages necessary to decrease the germination percentage to the values mentioned vary in Victory oats (water content 13 % in the treated kernels) from about 45000 to 55000 r (Table 1). In di-, tetra- and hexaploid wheat, at a water content of about 9 % in the kernels, the optimal dosages have not yet been reached (Table 2), but some evidence was obtained that the tetraploid *Triticum durum* was more resistant to X-ray treatment than the diploid *Tr. monococcum*.

Further researches are planned to supplement the data given here, which are to be regarded as preliminary results. These subsequent researches will also include di- and tetraploid oats.

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STUDIEN ÜBER EINE SPONTANE CHLORINA-MUTATION IN AVENA SATIVA

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(With a Summary in English)

EINLEITUNG.

IN der Nachkommenschaft einer Elitepflanze von der Sorte Goldregenhafer wurde im Jahre 1928 bei der gewöhnlichen Beobachtung über das Aufgehen der Haferversuche im Frühjahr auf den Svalöfer Zuchtfeldern eine bezüglich der Chlorophyllausbildung stark abweichende neue Sippe, forma *chlorina*, von ÅKERMAN gefunden. Der Goldregenhafer (auch Goldregen I genannt) ist eine alte Pedigreesorte, welche schon im Jahre 1892 von Professor N. HJALMAR NILSSON hier in Svalöf aus dem Miltonhafer ausgelesen wurde (N. HJ. NILSSON, 1894; ÅKERMAN, 1928). Der Miltonhafer war eine Mischsorte vom Probsteiertypus. Die Sorte Goldregenhafer war von Anfang an konstant. Von 1915 an, wo ÅKERMAN die Leitung der Züchtungsarbeiten mit Hafer übernahm, ist eine grosse Anzahl von Nachkommenschaften aus Einzelpflanzen dieser Sorte von ihm untersucht worden. Diese waren alle, abgesehen von ein Paar spontanen Einkreuzungen, mit dem alten Goldregen völlig identisch.

Im Jahre 1928 aber wurde in der Nachkommenschaft von einer 1926 ausgelesenen Elitepflanze eine deutliche Spaltung der Blattfarbe konstatiert. Von 45 Pflanzen waren nämlich 33 normal grün, während 12 dagegen eine gelblich grüne Farbe hatten. Das Verhältnis zwischen den beiden Typen lag also sehr nahe an 3 : 1 mit Dominanz für grün. Der Unterschied zwischen ihnen war im Keimpflanzenstadium sehr deutlich und leicht festzustellen. Je älter die Blätter der gelblichen Sippe wurden, desto grüner wurden sie. Das Ergrünen erfolgte ziemlich rasch, und die anfangs gelbgrünen Pflanzen nahmen eine reine, wenn auch helle, grüne Farbe an. Die neuentstandene Sippe erinnerte betreffs des Ergrünens also an die von CORRENS beschriebene *versicolor*-Sippe von *Mercurialis annua* (CORRENS, 1920). Die neue chlorophylldefekte Hafersippe könnte deshalb auch *versicolor* genannt werden. Da aber bei der Gerste ähnliche Sippen auf

dem Mutationswege spontan aufgetreten und von NILSSON-EHLE mit dem Namen *chlorina* bezeichnet worden sind (1922), scheint es am richtigsten, die gelbgrüne Hafersippe als f. *chlorina* zu bezeichnen. Ähnliche Sippen hat man auch bei *Sorghum* (KARPER and CONNER, 1931), *Vicia faba* (SIRKS, 1932) und *Oryza sativa* (KANNA, 1935) gefunden. In einem Vortrag über Letalfaktoren beim Hafer und Weizen wurde diese Sippe von ÅKERMAN ganz kurz erwähnt (ÅKERMAN, 1929). Sie wurde schon damals als f. *chlorina* bezeichnet. Später, in einem Aufsatz über die Vererbung des Ligulamerkmals beim Hafer, wurde dieselbe Sippe auch kurz erwähnt (ÅKERMAN und MÜHLOW, 1933), diesmal jedoch »vorläufig als *chlorina* oder *virescens*» (l. c. p. 141) benannt. Die Bezeichnung *chlorina* dürfte in ihrem jetzigen Umfang etwa die gelbgrünen Sippen umfassen, die überwiegend im Keimpflanzenstadium die gelbgrüne Farbe deutlich zeigen und dann diese Farbe entweder weiter in der Entwicklung behalten oder sie in mehr oder weniger gesättigtes Normalgrün zu verwandeln vermögen. Innerhalb dieser Abgrenzung des Begriffes *chlorina* können dann weiter eingehendere Benennungen der verschiedenen *chlorina*-Formen angewandt werden. Im hier vorliegenden Falle könnte vielleicht an einen Namen wie »chlorino-virescens» oder ähnliches gedacht werden. Wir haben indessen darauf verzichtet. Die Bezeichnung *virescens* (»ergrünend») allein dürfte eigentlich den Chlorophyllaberranten zugelegt werden, die rein weiss oder weissgrün in der ersten Entwicklung sind und dann ergrünen. Solche Typen sind in Menge bei Gerste aufgetreten und neulich auch in einer interessanten Form 1939 von FRÖIER in *Avena sativa* gefunden worden (noch nicht publiziert) und als f. *albovirescens* bezeichnet. Die Bezeichnung *versicolor* endlich (»farbwechselnd» oder auch »bunt») würde mit der jetzigen grossen Zahl bekannter Chlorophyllaberranten eine Mehrzahl schon gut gegen einander abgegrenzte Formkreise umfassen, was nicht zweckmässig wäre.

MORPHOLOGISCHE UND PHYSIOLOGISCHE EIGENSCHAFTEN DER CHLORINA-PFLANZEN.

Das Ergrünen der *chlorina*-Sippe scheint unter verschiedenen äusseren Verhältnissen ungleich schnell zu verlaufen. Wenigstens war dies im Frühjahr 1932 besonders ausgeprägt der Fall. Als das erste Blatt der *chlorina*-Pflanze sich entfaltete, waren die Witterungsverhältnisse sehr günstig. Bei sehr guten Bedingungen wurde dieses Jahr

die Aussaat des Hafermaterials bei hoher Bodenfeuchtigkeit und optimaler Bodenbearbeitung vorgenommen. Vor allem war die Temperatur für die Jahreszeit ungewöhnlich hoch. Von Mitte April bis 22. Mai war die mittlere Temperatur pro 24 Stunden gerechnet etwa 0,5° C. höher als normal. Am 23. Mai fiel die Temperatur aber ganz bedeutend im Zusammenhang mit dem Eintreten von trübem, regnerischem Wetter. Das zweite Blatt, welches sich während dieser Periode entfaltete, blieb viel länger gelblich als das erste. Ähnliche Beobachtungen haben wir in späteren Jahren auch machen können. Besonders in sehr trockenen Jahren, wo in der Zeit zwischen der Entfaltung des ersten bis vierten Blattes ungewöhnlich geringe Feuchtigkeit fiel — wie in 1939 und jetzt, in 1940 — hat sich die *chlorina*-Sippe in ihrem Wachstum als ungewöhnlich verzögert gezeigt, dies allem Anschein nach mit einem längeren Beharren der Blätter in dem gelbgrünen Zustand verknüpft.

Ältere *chlorina*-Pflanzen, welche geschosst haben, sehen gewöhnlich völlig normal grün aus und sind hinsichtlich der Blattfarbe nicht von normalen grünen Goldregenhaferpflanzen zu unterscheiden. Sie sind aber bedeutend kleiner und schwächer. Dies ist schon im Keimpflanzenstadium zu bemerken. Um diesen Unterschied zahlenmässig festzustellen, wurde im Frühling 1932 das Gewicht von Pflanzen der beiden Typen gemessen. Die Pflanzen stammten aus Kulturen, welche in kleinen Holzkästchen unter ganz gleichmässigen Verhältnissen aufgezogen wurden. Sie wurden mit einer Schere unmittelbar oberhalb der Erde abgeschnitten und gewogen. Die Pflanzen waren in diesem Stadium ganz klein und hatten nur die ersten zwei Blätter entwickelt. Abgeschnitten und gewogen wurden nur Pflanzen, die aus entweder konstant normalgrünen Einzelpflanzennachkommenschaften oder aus konstant gelblichgrünen stammten. Es wurden also nicht Pflanzen aus spaltenden Familien untersucht; dies, weil man dabei wenigstens in vereinzelten Fällen bei dem Markieren der normalgrünen Pflanzen auch versehentlich eine oder andere *chlorina*-Pflanze mitbekommen kann, die ungewöhnlich grün ist und also phenotypisch nicht so leicht von typischen normalgrünen Keimpflanzen unterscheidbar. Drei gelbgrüne Familien und drei rein grüne kamen zur Untersuchung.

Die mittleren Pflanzengewichte der drei normalgrünen Familien waren 0,10 Gr. (± 3,3 %), 0,11 Gr. (± 3,1 %) und 0,09 Gr. (± 4,1 %); diejenige der drei Familien von *chlorina*-Pflanzen waren 0,08 Gr. (± 4,1 %), 0,08 Gr. (± 3,4 %) und 0,07 Gr. (± 4,1 %). Da in den Kästchen, die etwa drei oder sogar vier Familien fassen konnten, sehr

gleichförmige Bedingungen in diesem Versuch vorhanden waren, sind die Versuchsverhältnisse damit bei der Betrachtung denen gleichgestellt worden, die auf dem freien Felde bei gleichförmigen Bodenbedingungen auftreten könnten. Und zwar würde unter diesen Bedingungen eine Aufteilung in »Blöcke» mit Berücksichtigung der Variation innerhalb des Blockes nicht nötig sein, weshalb sie auch hier weggelassen ist. Auf Grund der gleichmässigen Versuchsbedingungen kann man bei der statistischen Betrachtung der obenstehenden Messungsresultate das Material in zwei Gruppen aufteilen, was ja auch die biologische Betrachtung befriedigt, teils die normalgrünen Familien für sich als die eine Gruppe, teils die *chlorina*-Familien für sich als eine zweite Gruppe. Das Berechtigte einer solchen Gruppierung zeigt eine Varianzanalyse der sechs Familien. Wenn man nämlich mit FISHER (1938) die drei normalgrünen Familien in bezug auf »inter-class variance» (Zwischen-Klassenvarianze) und »intra-class variance» (Binnen-Klassenvarianze) untersucht, findet man hier die erstere viel kleiner als die letztere, d. h. die drei Familien gehören derselben statistischen Population an. Bei der Varianzanalyse der drei *chlorina*-Familien findet man ganz dasselbe. Auch ein Blick auf die Variationskurven der sechs Familien zeigt deutlich genug die Übereinstimmung der drei normalen Familien einerseits und der drei gelbgrünen andererseits. Diese Kurven sind hier nicht wiedergegeben worden. Dagegen sind die zwei Kurven, die die Variation der Gewichte aller zusammengenommenen normalgrünen (295 St.) und aller gelbgrünen Pflanzen (265 St.) repräsentieren, in Fig. 1 abgedruckt. Die Klassenweite ist hier 0,025 Gr.; eine geringere Klassenweite könnte mit Rücksicht auf den Wägungsfehler hier nicht zu Verwendung kommen. Wie aus Fig. 1 ersichtlich ist, gruppieren sich die betreffenden Varianten annähernd nach Zufallskurven. Die *chlorina*-Kurve zeigt auffallende Symmetrie. Die Kurve der normalgrünen 295 Pflanzen hat einen etwas unsymmetrischen Verlauf; wenn man die hier gefundenen Klassenwerte mit den nach der Zufallskurve theoretisch berechneten vergleicht, erhält man:

Gefunden	0	10	28	57	78	73	43	6	0
Erwartet	1	9	31	65	83	65	31	9	1
Klasse	*0*	*I*	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*

Eine Untersuchung der Abweichungen von der erwarteten Verteilung gemäss der Binomialkurve mit Hilfe der χ^2-Methode zeigt aber, dass die Abweichungen ohne signifikante Bedeutung sind; in 10—20 %

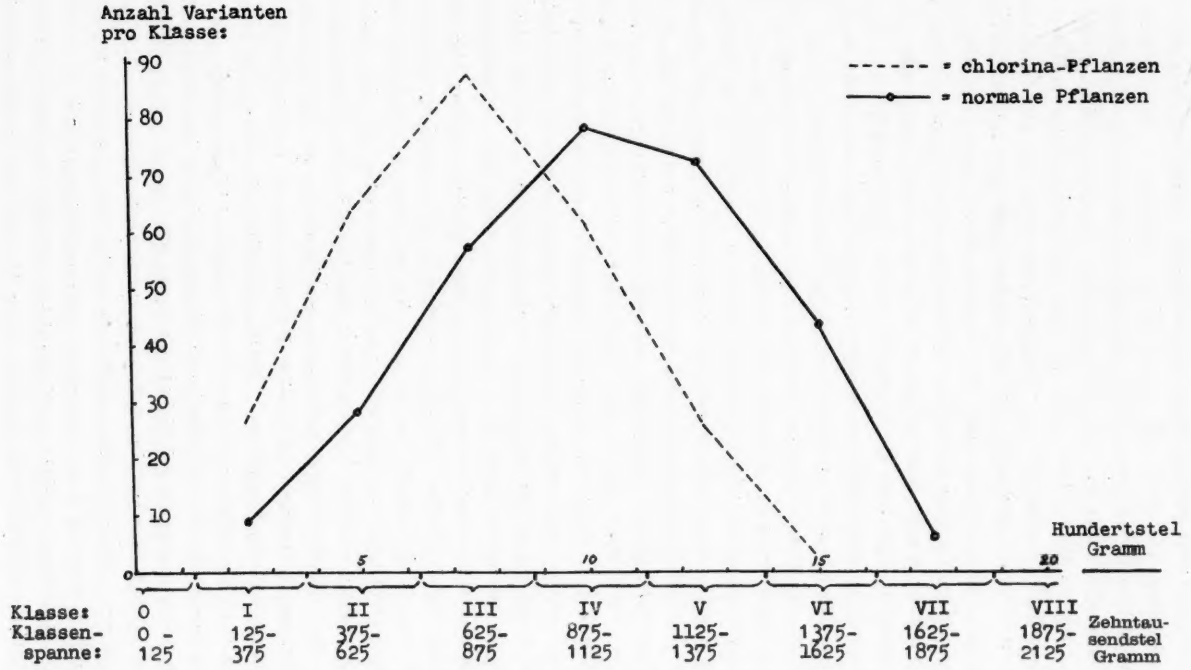

Fig. 1. Variationskurven der Pflanzengewichte von *chlorina*-Pflanzen und normalgrünen Pflanzen aus konstanten Nachkommenschaften im frühen Zweiblattstadium.

aller Fälle könnten nach dieser Untersuchung ähnliche $\Sigma\chi^2$-Werte erhalten werden.

Das mittlere Pflanzengewicht der normalgrünen Pflanzen beträgt $0{,}101 \pm 0{,}00200$ (2,0 %) Gr. Für die *chlorina*-Pflanzen ist das entsprechende Gewicht $0{,}075 \pm 0{,}00173$ (2,3 %) Gr. Da man hier die unbedeutende korrelierte Variabilität der beiden Variantenserien auf Grund der gewählten Versuchsbedingungen unberücksichtigt lassen kann, erhält man $M_{Diff.} = 0{,}026 \pm 0{,}00265$ (10,2 %) als Unterschied der beiden Mittelzahlen berechnet. Der mittlere Unterschied zwischen normalen und *chlorina*-Pflanzen auf dem frühen Zweiblattstadium beträgt also rund zwei Hundertstel bis drei Hundertstel Gramm (= 20 bis 30 %); dieser Unterschied ist statistisch sichergestellt. Der gefundene Unterschied übersteigt nämlich den mittleren Fehler beinahe zehnfach.

Schon auf diesem frühen Zweiblattstadium sind also die *chlorina*-Pflanzen in ihrer Entwicklung den Normalgrünen unterlegen. Der Unterschied ist zwar nicht grösser, als dass hierfür die schlechtere Herkunft der *chlorina*-Familien als Ursache herangezogen werden könnte. Im Durchschnitt entwickeln sich, wie unten gezeigt wird, die *chlorina*-Pflanzen bedeutend schwächer als die normalgrünen; damit ist auch eine schwächere Ausbildung der Karyopsen höchstwahrscheinlich verbunden. Um hier feststellen zu können, ob und in welchem Grade eine genetisch bedingte Verschiedenheit in Assimilationsintensität schon auf diesem Stadium vorliegt und die Entwicklung beeinflusst, müssen direkte Assimilations- und Respirationsuntersuchungen vorgenommen werden. In dem physiologischen Laboratorium des Schwedischen Saatzuchtvereins ist die *chlorina*-Sippe auch von diesen Gesichtspunkten untersucht worden (ANDERSSON und FRÖIER; noch nicht veröffentlicht). Die erwähnten physiologischen Untersuchungen werden laufend Blatt für Blatt in der Pflanzenontogenese der *chlorina*-Sippe unternommen in direktem Vergleich mit entsprechenden Blättern normaler Pflanzen unter Berücksichtigung möglichst gleicher Blattgrösse (Blattoberfläche); bei den bisherigen Arbeiten sind nur Blätter höherer Ordnung zur Untersuchung gekommen; da man hier die Assimilationsverhältnisse im freien Felde unter normalen Bedingungen möglichst erfassen will, kommen die Blätter niedrigerer Ordnung erst im Jahre 1941 zur Untersuchung.

In der weiteren Entwicklung der *chlorina*-Pflanzen tritt im Vergleich mit normalen Pflanzen eine Hemmung allmählich ein. Eine ähnliche Bestimmung des Durchschnittsgewichtes wie oben erwähnt wurde auf dem Vierblattstadium in einer 3 : 1-spaltenden Parzelle der

Kreuzung *chlorina* × Normaltypus der Sorte 0101 (aus der Sorte »Jaune géant à grâppes» — ihrerseits aus Gelber Flandrischer Hafer erhalten — stammend) ausgeführt. In diesem Falle hatten die grünen Pflanzen (Homo- und Heterozygoten) ein Durchschnittsgewicht von $0{,}72 \pm 0{,}02$ Gr., während die rezessiven *chlorina*-Homozygoten nur ein Gewicht von $0{,}24 \pm 0{,}12$ Gr. zeigten, also ein Unterschied von $0{,}48 \pm \pm 0{,}025$ Gr. oder in Prozent ausgedrückt, $200 \pm 10{,}4$ %.

Dieser Unterschied zwischen den beiden Typen, der höchstwahrscheinlich auf einer schwächeren Assimilationsintensität der *chlorina*-Pflanzen beruht, tritt ebenfalls bei reifen Pflanzen sehr deutlich hervor. Von 38 im Jahre 1930 ganz zufällig gewählten reifen normalgrünen Pflanzen aus konstant grünen Nachkommenschaften war das mittlere Gewicht der Pflanzen $8{,}2 \pm 0{,}40$ Gr. Um das Gewicht der Pflanzen zu bestimmen, wurden sie unmittelbar oberhalb des Wurzelhalses abgeschnitten. Randpflanzen wurden in den Wägungen nicht mitgenommen, weil sie 200 bis 300 % kräftigere Entwicklung als das Durchschnittsgewicht zeigten. Von 53 in der gleichen Art ausgewählten *chlorina*-Pflanzen aus konstanten Nachkommenschaften war das mittlere Gewicht nur $5{,}1 \pm 0{,}35$ Gr., also etwa 38 % niedriger als bei den normalgrünen Pflanzen.

Die ebenerwähnten Zahlen beziehen sich auf Pflanzen je für sich angebauter konstanter Nachkommenschaften der beiden Typen. Es wurde aber auch das Gewicht von grünen und gelbgrünen Pflanzen in spaltenden Beständen festgestellt. Die spaltenden Parzellen lagen hier auf einem besonders guten Bodenstück des Versuchsfeldes, weshalb die normalgrünen Pflanzen hier ein Durchschnittsgewicht (18 Pfl.) von $18{,}8 \pm 1{,}71$ Gr. erreichten. Die zwischen den normalgrünen wachsenden *chlorina*-Pflanzen, die in derselben Parzelle ausspalteten, zeigten ein Durchschnittsgewicht (23 Pfl.) von nur $1{,}8 \pm 0{,}37$ Gr. Hier war der Unterschied zwischen den beiden Typen also viel grösser als im vorigen Fall, was wahrscheinlich damit zusammenhing, dass die schwachen *chlorina*-Pflanzen von den normalgrünen, schneller wachsenden unterdrückt wurden. Die Bestockungsfähigkeit der *chlorina*-Pflanzen ist im Vergleich mit der von normalen Pflanzen gering. Dies gilt schon für *chlorina*-Bestände konstanter Nachkommenschaften und also, wie zu erwarten ist, in noch erhöhtem Grad für *chlorina*-Pflanzen in spaltenden Beständen, wo die Unterdrückung seitens der normalen Homo- und Heterozygoten hinzukommt. In Fig. 2 sind links zwei konstante *chlorina*-Nachkommenschaften (Reihe links zur Kreuzung herangezogen) abgebildet; rechts eine 3 : 1 spaltende Nachkommen-

schaft. In diesen Parzellen ist in jeder Reihe die Pflanzenzahl 30 (Abstand 5 Cm.), und der Abstand zwischen den Reihen ist 12,5 Cm., zwischen verschiedenen Parzellen 25 Cm. Die Unterschiede in Bestockungsfähigkeit treten in der Figur ganz klar zutage. Auch unter sehr günstigen Verhältnissen pflegen im konstanten *chlorina*-Bestand selten mehr als 2, höchstens 3 Halme entwickelt werden. Von diesen Halmen hat der am spätesten entwickelte immer den Charakter eines

Fig. 2. Links zwei einreihige Parzellen von konstanten *chlorina*-Nachkommenschaften; erste Reihe links zur Kreuzung herangezogen. Rechts 3 : 1-spaltende Parzelle (nur die Hälfte ersichtlich). — Photo H. OLSSON.

sehr späten, nicht zu voller Reife kommenden Nachtriebes. Im 3 : 1-spaltenden Bestand entwickelt eine *chlorina*-Pflanze nur äusserst selten mehr als einen Halm; wenn sich aber zwei entwickeln, gelangt der spätere fast nie zur Reife.

Die Länge der Halme mit voll entwickelten Rispen kann bei verhältnismässig freistehenden *chlorina*-Pflanzen dieselben Werte erreichen wie bei normalen Pflanzen (siehe Fig. 2, mittlere Parzelle!). In der Regel bleiben aber die Halme der gelbgrünen Rezessivhomozygoten,

was die Länge betrifft, hinter denen der normalgrünen Homo- und Heterozygoten zurück. Bei dem früher erwähnten (S. 377) Vergleich zwischen normalgrünen und gelbgrünen Pflanzen aus konstanten Nachkommenschaften variierte die Halmbündellänge der normalgrünen Pflanzen bei der Reife zwischen 117 und 118 Cm., die der *chlorina*-Pflanzen dagegen zwischen 103 und 105 Cm. Dieser Unterschied wird in spaltenden Beständen noch ausgeprägter. Hier wird indessen infolge des verschiedenen Entwicklungsgrades der unterdrückenden, raschwüchsigen normalen Pflanzen eine so grosse Höhenvariation der *chlorina*-Pflanzen hervorgerufen, dass man z. B. in sol-

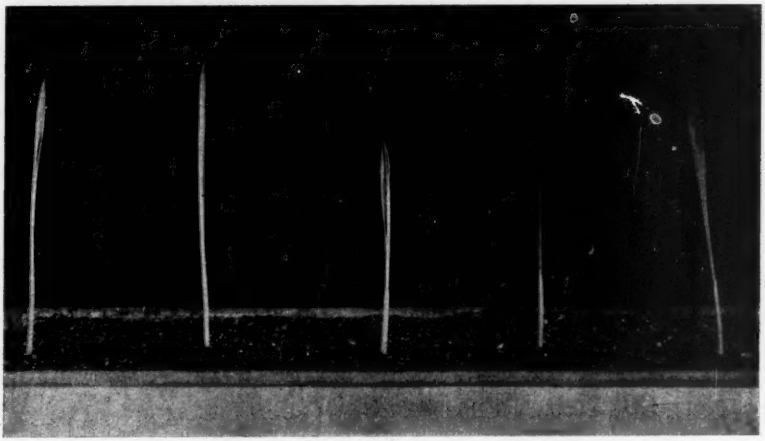

Fig. 3. Links drei Keimlinge von konstanten *chlorina*-Nachkommenschaften, rechts zwei von normalen Goldregenhaferpflanzen; alle 14 Tage alt. — Photo H. OLSSON.

chen spaltenden Parzellen Pflanzen in der Höhe von nur 30—40 Cm. (mit vollgebildeten Rispen) finden kann, während die Mittelhöhe der Halme von den Normalpflanzen 110 Cm. beträgt. In derselben Parzelle kann man indessen auch *chlorina*-Pflanzen von gut 100 Cm. Länge finden (nicht nur Randpflanzen!), die infolge besserer Licht- und Raumverhältnisse zu einer guten Entwicklung gelangt sind.

Eine Illustration zu der oben dargelegten verschiedenen Entwicklungsgeschwindigkeit der normalen und gelbgrünen Sippe von Goldregenhafer I bieten Fig. 3 und 4.

Die fünf Körner haben annähernd mit derselben Schnelligkeit gekeimt, und in Fig. 3 ist die photographische Aufnahme 14 Tage nach der Aussaat gemacht worden (Eisenberger Ultrarapidplatte; ohne

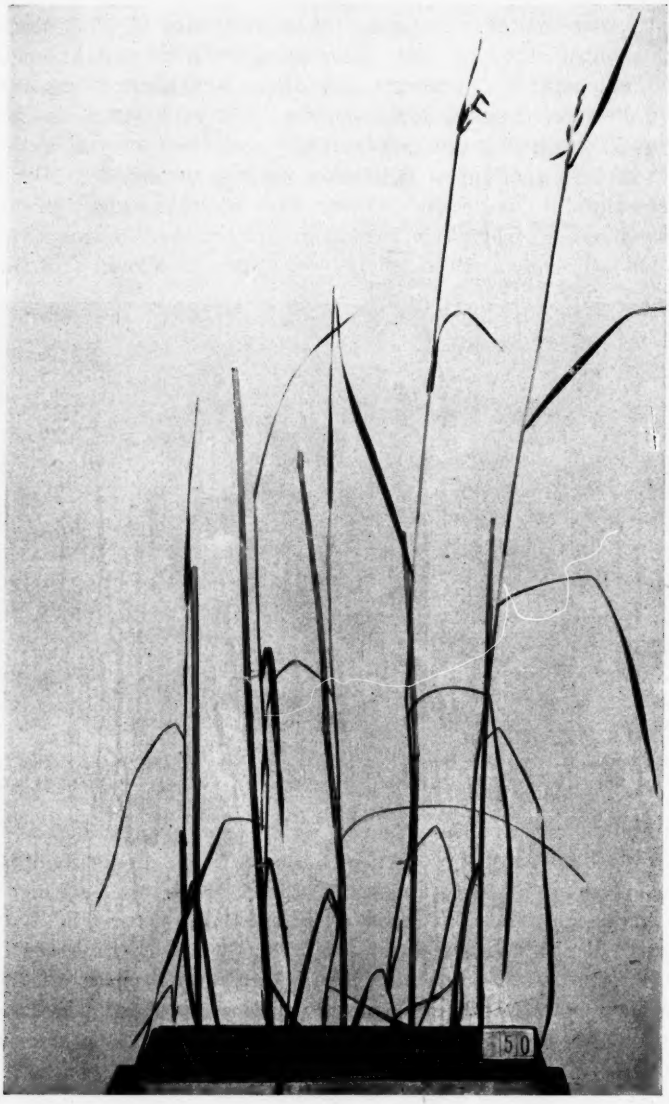

Fig. 4. Dieselben Pflanzen wie in Fig. 3, 50 Tage nach der Aussaat, in künstlicher Beleuchtung aufgezogen (siehe Text!). — Photo H. OLSSON.

Farbenfilter). Das erste Blatt der *chlorina*-Keimlinge war hier ganz gleichmässig hell gelbgrün, das der normalen gesättigt grün. Die weitere Entwicklung der fünf Pflanzen verlief unter künstlicher Beleuchtung im Frühling 1940 im Gewächshaus, wobei 1000-Watt-Lampen in 2 M. Entfernung als Lichtquelle dienten. Nach fünfzig Tagen von der Aussaat gerechnet wurde die Aufnahme in Fig. 4 genommen. Die normalen Pflanzen waren dann gerade in der Rispenentwicklung begriffen. Die starke Streckung des obersten Internodiums der *chlorina*-Pflanzen im Zusammenhang mit der Rispenausbildung hatte dagegen noch nicht begonnen. Bei den letztgenannten Pflanzen war in diesem Stadium nur das oberste Blatt ziemlich gelbgrün; alle unteren hatten gleich gesättigte normale Farbe wie sämtliche Blätter der normalen Pflanzen angenommen. Obwohl das Wachstum im Gewächshaus sich in vielen Hinsichten von dem auf dem freien Felde unterscheidet, stimmte das Ergrünen der Blätter in diesem kleinen Versuch doch im Wesentlichen mit dem entsprechenden Vorgang auf dem Felde überein, dies wenigstens was die vier ersten Blätter betrifft.

Unter anderen Beobachtungen, die bei dieser *chlorina*-Sippe seit ihrem Auftreten gemacht worden sind, verdient im Zusammenhang mit der anfangs schwächeren Ausbildung ihrer Blätter auch genannt zu werden, dass wir mehrmals die Beobachtung machen konnten, dass die Blätter bei starkem Wind leichter geknickt werden als die der normalen Pflanzen. Die Ursache dürfte hier in der langsameren Entwicklung der Stützgewebe des Blattes zu suchen sein. Wenn nämlich die *chlorina*-Blätter älter werden und volle grüne Farbe erreicht haben, scheinen sie dagegen nicht brüchiger als die gleichaltrigen, normalen Blätter zu sein. Eine nachfolgende anatomische Untersuchung mit gleichzeitiger Bestimmung der Art von Chlorophylldistribution und Gehalt an Rohchlorophyll ist im Anschluss an die erwähnten Assimilationsuntersuchungen von ANDERSSON und FRÖIER begonnen worden.

Es verdient betreffs der Assimilationsintensität dieser chlorophylldefekten Hafersippe noch eine Beobachtung erwähnt zu werden. ÅKERMAN machte im Jahre 1932 einen Versuch mit Exposition der jungen *chlorina*-Pflanzen in geschwächtem Licht, dazu von den interessanten Befunden bei der *lutescens*-Sippe von *Avena sativa* veranlasst (ÅKERMAN, 1922). Bei der letztgenannten »Chlorophyllsippe» war die Rezessivhomozygote, f. *lutescens*, im gewöhnlichen Tageslichte nur sehr kurze Zeit lebensfähig: bei vermindertem Tageslicht konnten die rezessiven Pflanzen indessen mehrere Monate am Leben erhalten werden, d. h. die sonst letale Form konnte bei dieser verminderten

Lichtintensität einigermassen befriedigend assimilieren. Für die oben erwähnten Wägungsversuche wurden *chlorina*-Pflanzen (konstante Nachkommenschaften) in kleine Kästchen ausgepflanzt. In der ersten Juniwoche 1932 hatten die Pflanzen das Zweiblattstadium erreicht. Von 8 Kästchen mit *chlorina*-Nachkommenschaften wurden am $^{11}/_{6}$ 4 unter kalkbreibestrichenes Fensterglas im Kaltbeet gestellt; 4 standen zu derselben Zeit neben dem Kaltbeet im Freien. Am $^{14}/_{6}$ war schon ein deutlicher Unterschied zu bemerken. Die Pflanzen in den Kaltbeetkästchen zeigten eine etwas dunklere grüne Farbe als die dem ungedämpften Tageslicht ausgesetzten. Auf Grund von Verbrauch mehrerer Pflanzen zwecks Wägungen wurde der Versuch nicht weiter fortgeführt. Immerhin gibt diese vereinzelte Beobachtung vielleicht eine Andeutung auf Verschiedenheiten in dem dynamischen Reaktionssystem des Chlorophylls der *chlorina*-Blätter bei verschiedenen Lichtintensitäten. Insbesondere wäre von Interesse, die Chlorophyllausbildung und die Assimilationsvorgänge der *chlorina*-Blätter bei verschiedenen schwachen Lichtintensitäten (500—1500 Lux) zu untersuchen. Die Methodik der Assimilationsuntersuchungen, in sich nunmehr recht gut ausgearbeitet, leidet aber an dem nicht leicht zu vermeidenden Übel, dass bei so schwachen Lichtintensitäten wie die hier in Frage kommenden die Spaltöffnungsvorgänge schwer zu kontrollieren sind, weshalb derartige Untersuchungen zur Zeit noch zu den schwierigsten auf dem Gebiete der Pflanzenassimilation gerechnet werden müssen.

GENETISCHE ANALYSE.

Um die Vererbung dieser chlorophylldefekten Sippe näher zu verfolgen, wurden im Jahre 1929 zum ersten Male mehrere Nachkommenschaften der beiden Typen aufgezogen. Die dabei erhaltenen Spaltungszahlen sind in Tabelle 1 zusammengefasst worden. Die Nachkommen der gelblichen Pflanzen waren alle wie erwartet konstant gelblich. In drei von denjenigen Nachkommenschaften dagegen, welche aus grünen Mutterpflanzen stammten, kam Spaltung im Verhältnis 123 normalgrüne : 35 gelbgrünen Pflanzen vor, was mit dem erwarteten Verhältnis 3 : 1 gut übereinstimmt.

In den Jahren 1930 und 1932 wurden wieder einige Nachkommen hiervon aufgezogen ebenso auch von 1935 an jedes Jahr bis 1940, dies um Material für Observations- und Demonstrationszwecke, Kreuzungen u. s. w. zur Verfügung zu haben. In Tabelle 2 sind die Spal-

tungszahlen der verschiedenen Jahrgänge zusammengeführt worden. Die Aufrechnungen der Spaltungen betreffen also D_3 bis D_{10}.

Die einfache Betrachtung der Totalsummen (D_3—D_{10}) am Ende der Tabelle 2 zeigt anfangs keine gute Übereinstimmung der Spaltungszahlen mit dem erwarteten Verhältnis 3 : 1. Ein Defizit von Rezessivhomozygoten, das beträchtlich ist und das den Wert D/m auf 5,6 aufgetrieben hat, ist hier vorhanden. Nun kann man sich fragen, ob unter den untersuchten Nachkommenschaften solche sind, die ausserhalb

TABELLE 1. *Nachkommenschaften in D_2.*

Aussehen der Elternpflanze	Feldnummer 1929	Beobachtet		Erwartet nach 3 : 1		D	m	D/m
		grün	*chlorina*	grün	*chlorina*			
Gelbgrün...	927 b_1	—	16	—	—	—	—	—
»	2	—	10	—	—	—	—	—
»	3	—	6	—	—	—	—	—
»	4	—	9	—	—	—	—	—
»	5	—	14	—	—	—	—	—
»	6	—	38	—	—	—	—	—
Grün.....	7	62	19	60,8	20,2	— 1,2	± 3,90	0,3
»	8	34	6	30,0	10,0	— 4,0	± 2,74	1,5
»	9	27	10	27,7	9,3	+ 0,7	± 2,64	2,7
»	10	62	—	—	—	—	—	—
»	11	63	—	—	—	—	—	—
Summe der spaltenden Nachkommenschaften	—	123	35	118,5	39,5	— 4,5	± 5,44	0,8

der zufallsmässigen Variation fallen, oder anders ausgedrückt, Nachkommenschaften, die ein grösseres Defizit an *chlorina*-Pflanzen zeigen, als nur durch zufällige Variation verursacht werden könnte. Die nähere statistische Betrachtung muss hier die verschiedenen Jahrgänge vereinzelt behandeln; auf eine Analyse der $\Sigma\chi^2$ jedes mehr abweichenden Jahrganges gehen wir also zunächst ein.

Es zeigt sich bei dem Überblick der Werte auf D/m, $\Sigma\chi^2$ und P in den drei Jahren 1932, 1936 und 1938, dass in diesen Jahrgängen die bedeutendsten Abweichungen vom Verhältnis 3 : 1 zu finden sind.

Für 1932 haben wir D/m = 3,7, $\Sigma\chi^2 = 12{,}412$ und $P > 0{,}05$. Wenn wir mit FISHER $P = 0{,}05$ als eine praktische Grenze für die Signifikanz der Resultate betrachten, würden also die Abweichungen vom Verhältnis 3 : 1 im Jahre 1932 nur auf reinem Zufall bei der beschränkten Zahl der Nachkommenschaften beruhen. Dasselbe finden wir für das Jahr 1936, wo D/m = 3,0, $\Sigma\chi^2 = 20{,}664$ und $P > 0{,}10$ ist. Dagegen erhalten wir für das Jahr 1938: D/m = 5,2, $\Sigma\chi^2 = 38{,}424$ und $P < 0{,}01$, d. h. dieses Jahr kommen unter den Nachkommenschaften solche vor, die distinkt ausserhalb der rein zufallsmässigen Variation fallen.

In übrigen Jahrgängen variiert der Wert D/m zwischen so niedrigen Werten (1,9—0,2), dass wir hier die χ^2-Analyse unterlassen haben. Die nahe Übereinstimmung der Werte mit den theoretischen fallen besonders in den Jahren 1935 und 1939 auf.

Das Defizit an *chlorina*-Rezessiven in den Jahren 1932, 1936 und besonders 1938 — nur im letztgenannten Jahre statistisch sicher nachgewiesen! — mag, da Zertation oder gametische Letalität hier wahrscheinlich nicht in Frage kommt, auf hauptsächlich zwei Weisen entstanden sein. Entweder besitzen die Rezessivhomozygoten eine gewisse Letalität — ob schon embryonal bleibt noch eine offene Frage — da sie ja später in ihrer Entwicklung hinter den normalen Pflanzen zurück bleiben und sich allgemein unter ungünstigeren Bedingungen viel schwächer entwickeln als diese. Oder hat der in eben diesen drei genannten Jahren auftretende Fritfliegenbefall (*Oscinella frit* L.) die grösste Rolle gespielt. Obwohl die theoretischen Versuche möglichst früh gesät und auf Feldstücke gelegt werden, wo die Fritfliege selten oder wenig aufzutreten pflegt, konnte in den genannten Jahren ein gelinder Befall nicht vermieden werden. Insbesonders gilt dies für das Jahr 1938. Wir haben nun bei dieser *chlorina*-Sippe mehrmals beobachten können, dass die jungen *chlorina*-Pflanzen viel stärker als normale Pflanzen von der Fritfliege befallen werden: wenn der Befall bei sehr frühem Stadium eintritt, müssen wir den Schluss ziehen, dass die Fritfliegenschaden wesentlich zur Ausbildung des Defizits an *chlorina*-Pflanzen mitwirken können. Dies ist auch tatsächlich in 1938 der Fall gewesen (siehe Nachkommenschaften 967_7 und 967_{10}!). Der bisher allerstärkste Fritfliegenbefall in diesen theoretischen Parzellen trat in 1935 auf. Dieses Jahr kam der Befall indessen recht spät. Die Schädigungen trafen diesmal die *chlorina*-Pflanzen erst bei einem Stadium, wo sie so weit gekommen waren, dass sie bei der Aufzählung sicher als *chlorina*-Rezessive markiert werden konnten — obwohl sie sehr von der Fliege angegriffen waren! — und deshalb wurde 1935 eine sogar sehr gute

TABELLE 2. *Nachkommenschaften von grünen Pflanzen in D_3—D_{10}.*

Nummer der Mutterpflanze im nächst vorangehenden Anbaujahr	Feldnummer	Beobachtet		Erwartet nach 3 : 1		D	m	D/m
		grün	*chlorina*	grün	*chlorina*			
1929—927b$_{7a}$	*1930*—914$_{23}$	81	—	—	—	—	—	—
b	24	98	23	90,8	30,2	− 7,2	± 4,76	1,5
8a	25	59	11	52,5	17,5	− 6,5	± 3,62	1,8
b	26	49	12	45,7	15,3	− 3,3	± 3,39	1,0
c	27	53	21	55,5	18,5	+ 2,5	± 3,73	0,7
10a	28	99	—	—	—	—	—	—
b	29	90	—	—	—	—	—	—
c	30	107	—	—	—	—	—	—
Summe D_3	—	259	67	244,5	81,5	− 14,5	± 7,82	1,9
1930—914$_{25a}$	*1932*—922$_6$	122	32	115,5	38,5	− 6,5	± 5,37	1,2
b	7	70	18	66,0	22,0	− 4,0	± 4,06	1,0
c	8	200	57	192,7	64,3	− 7,3	± 6,94	1,1
d	9	211	51	196,5	65,5	− 14,5	± 7,01	2,1
e	10	135	26	120,7	40,3	− 14,3	± 5,50	2,6
f	11	154	—	—	—	—	—	—
g	12	72	18	67,5	22,5	− 4,5	± 4,11	1,1
h	13	227	67	220,5	73,5	− 6.5	± 7,42	0,9
Summe D_4	—	1037	269	979,5	326,5	− 57,5	± 15,65	3,7
1932—922$_{10a}$	*1935*—952$_1$	18	5	17,2	5,8	− 0,8	± 2,08	0,4
b	2	7	1	6,0	2,0	− 1,0	± 1,23	0,8
c	3	11	7	13,5	4,5	+ 2,5	± 1,84	1,4
d	4	47	5	39,0	13,0	− 8,0	± 3,12	2,6
e	5	11	7	13,5	4,5	− 1,0	± 1,23	0,8
f	6	16	4	15,0	5,0	− 1,0	± 1,94	0,5
g	7	51	17	51,0	17,0	± 0,0	± 3,57	0,0
h	8	43	22	48,7	16,3	+ 5,7	± 3,49	1,6
i	9	6	1	4,2	1,8	− 0,8	± 1,04	0,8
j	10	46	—	—	—	—	—	—
12a	11	8	1	6,7	2,3	− 1,3	± 1,31	1,0
b	12	47	13	45,0	15,0	− 2,0	± 3,35	0,6
c	13	28	10	28,5	9,5	+ 0,5	± 2,67	0,2
d	14	14	8	16,5	5,5	+ 2,5	± 2,03	1,2
e	15	30	5	26,2	8,8	− 3,8	± 2,57	1,5
f	16	93	—	—	—	—	—	—
g	17	48	13	45,7	15,3	− 2,3	± 3,39	0,7

Nummer der Mutterpflanze im nächst vorangehenden Anbaujahr	Feldnummer	Beobachtet		Erwartet nach 3 : 1		D	m	D/m
		grün	*chlorina*	grün	*chlorina*			
h	18	40	18	43,5	14,5	+ 3,5	± 3,30	1,1
i	19	19	3	16,5	5,5	− 2,5	± 2,03	1,2
j	20	1	2	2,2	0,8	+ 1,2	± 0,77	1,6
Summe D_5	—	445	142	440,2	146,8	− 4,8	± 10,49	0,5
1935—952_{1a}	*1936*—943_1	147	—	—	—	—	—	—
b	2	134	—	—	—	—	—	—
c	3	48	—	—	—	—	—	—
d	4	64	14	58,5	19,5	− 5,5	± 3,82	1,4
e	5	173	69	181,5	60,5	+ 8,5	± 6,74	1,3
f	6	96	34	97,5	32,5	+ 1,5	± 5,04	0,3
g	7	97	—	—	—	—	—	—
h	8	42	8	37,5	12,5	− 4,5	± 3,06	1,5
i	9	69	14	62,2	20,8	− 6,8	± 3,95	1,7
j	10	58	11	51,7	17,3	− 6,3	± 3,60	1,8
4a	11	114	—	—	—	—	—	—
b	12	34	6	30,0	10,0	− 4,0	± 2,74	1,5
c	13	54	16	52,5	17,5	− 1,5	± 3,62	0,4
d	14	49	—	—	—	—	—	—
e	15	71	26	72,7	24,3	+ 1,7	± 4,27	0,4
f	16	46	16	46,5	15,5	+ 0,5	± 4,03	0,1
g	17	192	50	181,5	60,5	− 10,5	± 6,74	1,6
h	18	121	26	110,2	36,8	− 10,8	± 5,25	2,1
i	19	65	15	60,0	20,0	− 5,0	± 3,87	1,3
j	20	56	10	49,5	16,5	− 6,5	± 3,52	1,8
k	21	58	14	54,0	18,0	− 4,0	± 3,67	1,1
l	22	194	—	—	—	—	—	—
m	23	42	—	—	—	—	—	—
n	24	12	5	12,7	4,3	+ 0,7	± 1,79	0,4
o	25	33	12	33,7	11,3	+ 0,7	± 2,91	0,2
Summe D_6	—	1244	346	1192,5	397,5	− 51,5	± 17,26	3,0
1936—943_{1a}	*1937*—956_6	36	—	—	—	—	—	—
d	9	8	—	—	—	—	—	—
e	10	49	17	49,5	16,5	+ 0,5	± 3,52	0,1
f	11	30	12	31,5	10,5	+ 1,5	± 2,81	0,5
g	12	40	16	42,0	14,0	+ 2,0	± 3,30	0,6
h	13	37	11	36,0	12,0	+ 1,0	± 3,00	0,3
i	14	46	—	—	—	—	—	—

Nummer der Mutterpflanze im nächst vorangehenden Anbaujahr	Feldnummer	Beobachtet		Erwartet nach 3 : 1		D	m	D/m
		grün	*chlorina*	grün	*chlorina*			
1936—943ij	*1937*—9561 5	63	—	—	—	—	—	—
k	16	14	2	12,0	4,0	— 2,0	± 1,73	1,2
l	17	38	15	39,7	13,3	+ 1,7	± 3,16	0,5
m	18	53	—	—	—	—	—	—
n	19	56	27	62,2	20,8	+ 6,2	± 3,95	1,6
o	20	50	22	54,0	18,0	+ 4,0	± 3,67	1,1
Summe D_7	—	314	122	327,0	109,0	+ 13,0	± 9,04	1,4
1937—956 10a	*1938*—967 3	13	4	12,7	4,3	— 0,3	± 1,79	0,2
b	4	57	17	55,5	18,5	— 1,5	± 3,73	0,4
c	5	113	31	108,0	36,0	— 5,0	± 5,20	1,0
d	6	60	11	53,2	17,8	— 6,8	± 3,65	1,9
e	7	75	5	60,0	20,0	— 15,0	± 3,87	3,9
f	8	7	1	6,0	2,0	— 1,0	± 1,23	0,8
g	9	33	8	29,7	10,3	— 2,3	± 2,73	0,8
h	10	48	10	43,5	14,5	— 4,5	± 3,30	1,4
i	11	40	13	39,7	13,3	— 0,3	± 3,16	0,1
j	12	51	11	46,5	15,5	— 4,5	± 3,41	1,3
17a	13	140	33	129,7	43,3	— 10,3	± 5,70	1,8
b	14	46	12	43,5	14,5	— 2,5	± 3,30	0,8
c	15	22	2	18,0	6,0	— 4,0	± 2,12	1,9
d	16	58	19	57,7	19,3	— 0,3	± 3,80	0,1
e	17	43	—	—	—	—	—	—
f	18	18	6	18,0	6,0	± 0,0	± 2,12	0,0
g	19	73	4	57,7	19,3	— 15,3	± 3,80	4,0
h	20	15	3	13,5	4,5	— 1,5	± 1,84	0,8
i	21	84	20	78,0	26,0	— 6,0	± 4,42	1,4
j	22	30	13	32,2	10,8	+ 2,2	± 2,84	0,8
Summe D_8	—	983	223	904,5	301,5	— 78,5	± 15,03	5,2
1938—967 6a	*1939*—953 3	61	27	66,0	22,0	+ 5,0	± 4,06	1,2
b	4	alle	—	—	—	—	—	—
c	5	33	11	33,0	11,0	± 0,0	± 2,87	0,0
d	6	48	20	51,0	17,0	+ 3,0	± 3,57	0,8
e	7	73	23	72,0	24,0	— 1,0	± 4,24	0,2
f	8	52	15	50,2	16,8	— 1,8	± 3,55	0,5
g	9	alle	—	—	—	—	—	—
h	10	40	14	40,5	13,5	+ 0,5	± 3,18	0,2
13a	11	94	25	89,2	29,8	— 4,8	± 4,73	1,0

Nummer der Mutterpflanze im nächst vorangehenden Anbaujahr	Feldnummer	Beobachtet		Erwartet nach 3 : 1		D	m	D/m
		grün	*chlorina*	grün	*chlorina*			
1938—967$_{13b}$	*1939*—953$_{12}$	alle	—	—	—	—	—	—
c	13	108	32	105,0	35,0	− 3,0	± 5,12	0,6
d	14	alle	—	—	—	—	—	—
e	15	76	28	78,0	26,0	+ 2,0	± 4,41	0,5
f	16	66	22	66,0	22,0	± 0,0	± 4,06	0,0
g	17	171	52	115,2	55,8	− 3,8	± 6,13	0,6
h	18	117	30	110,2	36,8	− 6,8	± 5,25	1,3
i	19	138	55	144,7	48,3	+ 6,7	± 6,02	1,1
Summe D_9	—	1077	354	1073,2	357,8	− 3,8	± 16,4	0,2
1939—953$_{3a}$	*1940*—953$_1$	74	23	72,7	24,3	− 1,3	± 4,27	0,3
b	2	30	11	30,7	10,3	+ 0,7	± 2,73	0,3
c	3	alle	—	—	—	—	—	—
d	4	alle	—	—	—	—	—	—
e	5	alle	—	—	—	—	—	—
f	6	69	19	66,0	22,0	− 3,0	± 4,06	0,7
g	7	107	34	105,7	35,3	− 1,3	± 5,14	0,3
h	8	98	24	91,5	30,5	− 6,5	± 4,78	1,4
i	9	alle	—	—	—	—	—	—
Summe D_{10}	—	378	111	366,7	122,3	− 11,3	± 9,58	1,2
Summe D_{3-10}	—	5737	1634	5528,2	1842,8	− 208,8	± 37,18	5,6

Übereinstimmung mit dem Verhältnis 3 : 1 erhalten, wie aus Tabelle 2 ersichtlich ist (D/m = 0,5).

In 1939 ist die Übereinstimmung mit 3 : 1 ebenfalls sehr gut. 1937 tritt zufallsmässig sogar ein kleiner Überschuss an *chlorina*-Pflanzen auf. Wenn man das Verhältnis zwischen spaltenden und nichtspaltenden Nachkommenschaften untersucht, findet man im Ganzen keine gute Übereinstimmung: auf 91 spaltende kommen nur 29 nichtspaltende. Nach 2 : 1 erwartet sollten 80 spaltende und 40 nichtspaltende auftreten. Bei der verhältnismässig begrenzten Zahl untersuchter Nachkommenschaften in jedem Jahr ist dies indessen erklärlich.

Man kann auf Grund der bisher erhaltenen Spaltungszahlen und mit Rücksichtnahme auf den mitwirkenden Fritfliegenbefall keine

sicheren Andeutungen auf eine Letalität der jungen *chlorina*-Keimpflanzen finden. Jedenfalls muss der Grad dieser Letalität schwach sein und unter guten Bedingungen der Umweltfaktoren (wie wahrscheinlich im Jahre 1935 und 1939) nicht zum Ausdruck kommen. Nur eine vergleichende Untersuchung des Keimungsverlaufes in sehr grossem Masstab dürfte diese Frage näher zur Lösung bringen.

ENTSTEHUNG DER CHLORINA-SIPPE.

Was die Entstehungsweise dieser neuen chlorophylldefekten Sippe betrifft, dürfte man wohl zunächst annehmen, dass sie durch irgend eine spontane Veränderung des Erbfaktorkomplexes für normale grüne Farbe zustandekommen sei. Spontane Kreuzung mit einer anderen Sorte als Ursache der Entstehung von der *chlorina*-Sippe kann nicht in Frage kommen, weil die sämtlichen ausgespalteten, normalgrünen Pflanzen identisch mit dem Goldregenhafer I übereinstimmen, was bei einer Kreuzung nicht möglich wäre. Und ausserdem wäre ja, wenn eine Kreuzung trotzdem vorläge, eine andere Spaltung als 3 : 1, wahrscheinlich 15 : 1 oder 63 : 1, in der ersten Nachkommenschaft zu erwarten.

Die fragliche, durch monofaktorielle Spaltung zum Anschein kommende Veränderung des Erbfaktorkomplexes für grüne Farbe muss schon im Jahre 1925 bei der Gametenbildung eingetroffen sein, denn die im Jahre 1926 ausgewählte Pflanze war eine Heterozygote zwischen normal grün und gelblich, die in der nächsten Generation im Jahre 1928 rein gelbliche Pflanzen im Verhältnis 1 gelblich auf 3 normalgrün ausspaltete.

Durch unsere Versuche wurde also wahrscheinlich gemacht, dass der Unterschied zwischen normalem, grünem Goldregenhafer I und der daraus erhaltenen gelblichen *chlorina*-Sippe nur auf einem mendelnden Faktor beruht. Es dürfte mit den heutigen, erweiterten Kenntnissen von den Mutationsvorgängen noch offen stehen, ob wir es hier mit einer echten »Genmutation» *sensu strictu* zu tun haben, d. h. Veränderung eines einzelnen Gens (im Genkomplex für normale Chlorophyllentwicklung), oder ob diese Veränderung auf einer geringen Chromosomenaberration (Translokation, Inversion, Deficiency u. a.) im normalen Genom beruht. Welcher Art die entstandene Veränderung nach diesen beiden Auffassungen auch sein möge, ist es jedoch sicher, dass sie sich ohne anschliessende Sterilitätserscheinungen durch mehrere Generationen unverändert vererbt, und weiter, dass die

chlorina-Sippe, mit anderen normalgrünen Hafersorten als Goldregen I gekreuzt, die Existenz von drei homomeren Erbfaktoren für die *chlorina*-Eigenschaft verrät, wie unten gezeigt wird.

KREUZUNGEN ZWISCHEN DER CHLORINA-SIPPE AUS GOLDREGENHAFER I UND ANDEREN HAFERSORTEN.

Wie aus den oben hervorgelegten Untersuchungen ersichtlich, kommt bei dem gewöhnlichen Svalöfs Goldregenhafer I ein Faktor vor, welcher die gelblich grüne Farbe der *chlorina*-Form in grün mit Dominanz verändert. Dieser dominante Faktor beim Goldregenhafer I bezeichnen wir als *Chlor 1*, und die Genformel der rezessiven, gelblich grünen Form wäre demgemäss, falls *n* solche homomere Faktoren existieren, *chlor 1 chlor 1, chlor 2 chlor 2, ... chlor n chlor n.*

Um das Vorkommen von diesem Faktor oder damit homomeren solchen bei anderen Hafersorten festzustellen, wurden im Jahre 1929 einige Kreuzungen zwischen der Mutationsform *chlor 1 chlor 1 . . . . chlor n chlor n* und einigen Sorten verschiedener Herkünfte und ökologischer Typen ausgeführt. Vor allem wurde dadurch versucht, die Frage zu beantworten, ob und in welcher Umfassung homomere Faktoren für diesen Chlorophylldefekten vorkommen. Für die von ÅKERMAN früher studierte *lutescens*-Form (ÅKERMAN, 1922) wurde bekanntlich das Vorhandensein von drei solchen Faktoren festgestellt. Das Studium der Polymerie ist ja aus mehreren Gesichtspunkten von Interesse, erstens, weil es natürlich immer von Bedeutung ist, ein grösseres Beobachtungsmaterial heranzuschaffen, um den Zusammenhang zwischen Polymerie und Polyploidie eingehender beleuchten zu können. Der Kulturhafer ist bekanntlich hexaploid (KIHARA, 1919) und, wie man erwarten konnte, ist das Vorkommen von Di- und Trimerie auch in mehreren Fällen schon konstatiert worden, wie z. B. in bezug auf die schwarze Spelzenfarbe (NILSSON-EHLE, 1909; ROBB, 1932), Ligulalosigkeit (NILSSON-EHLE, 1909; MEURMAN, 1926; ÅKERMAN und MÜHLOW, 1933), Rispentypus (NILSSON-EHLE, 1909; MEURMAN, 1926), Vergilbung der Blattfarbe bei Keimpflanzen, f. *lutescens* (ÅKERMAN, 1922). Trotzdem sind natürlich weitere Untersuchungen hierüber immer von Bedeutung, vor allem, wenn sie auf einer breiten Basis aufgebaut werden, so dass eine Mehrzahl von Kreuzungen mit befriedigend grossen Spaltungsgenerationen gründlich untersucht wird.

Zweitens beabsichtigen wir durch diese Untersuchungen den Zusammenhang zwischen Polymerie bzw. Polyploidie und Mutations-

frequenz näher zu studieren. Dass ein Zusammenhang in dieser Hinsicht besteht, ist schon mehrmals hervorgehoben worden; vgl. z. B. ÅKERMAN (1922), STADLER (1929) und HUSKINS (1933). Ein umfangreicheres Beobachtungsmaterial ist doch auch hier nötig, um den erwähnten Zusammenhang näher kennen zu lernen. Vor allem müssen möglichst viele Sorten untersucht werden, um eine statistische Auffassung von dem Vorkommen di- oder trimeren Formen zu erhalten, und natürlich müssen auch möglichst viele mutierende Eigenschaften in dieser Hinsicht untersucht werden.

Bei den Kreuzungen im Jahre 1929 wurde, wie oben gesagt, die *chlorina*-Mutation aus Goldregenhafer I mit folgenden fünf anderen Hafersorten gekreuzt: Siegeshafer, Abeds Novahafer, Glockenhafer II, Hedehafer, Linie 0101 (aus Jaune géant à grâppes).

Der *Siegeshafer* ist eine Schwestersorte des Goldregenhafers und stammt wie dieser aus dem Miltonhafer. Diese beiden Sorten wurden im Jahre 1892 von Professor N. HJ. NILSSON ausgelesen. Sie sind von Anfang an homozygot gewesen und sind also typische reine Linien. Dies ist auch mit dem *Abeds Novahafer* der Fall, welcher von dem dänischen Züchter H. A. B. VESTERGAARD aus einer deutschen Probsteiersorte, Riesen Sommerhafer genannt, als eine reine Linie ausgelesen wurde. *Glockenhafer II* ist eine schwarzkörnige Sorte, welche im Jahre 1898 im Goldregenhafer angetroffen wurde, und die allem Anschein nach aus einer spontanen Kreuzung stammt. Glockenhafer II ist seit fast drei Jahrzehnten augenscheinlich völlig konstant. Der *Hedehafer* ist eine reine Linie aus einem alten Landhafer von Jütland in Dänemark, vom alten Grauhafer-Typus (Spelzenhafer). Die *Linie 0101* stammt aus der Sorte Jaune géant à grâppes aus Gelber Flandrischer Hafer.

Von den Kreuzungen wurde folgendes Jahr, 1930, die F_1-Generation aufgezogen. Sämtliche Pflanzen in dieser waren grün und nicht von den normalgrünen Mutterpflanzen zu unterscheiden, weshalb also volle Dominanz vorlag. Die F_2-Generation konnte erst 1932 aufgezogen werden. Die in dieser Generation erhaltenen Spaltungszahlen sind in Tabelle 3 zusammengestellt worden. Die F_2-Generation lag zufällig auf einem sehr gleichförmigen Stück des Versuchsfeldes ohne Fritfliegenbefall, weshalb F_2 im Vergleich mit der D_4 in demselben Jahr von *chlorina*-spaltenden Goldregenhafer-Parzellen (siehe Tabelle 2, S. 385) viel bessere Übereinstimmung von den gefundenen mit den theoretischen Spaltungszahlen aufweist.

Schon beim ersten Blick auf Tabelle 3 sieht man, dass die Spal-

TABELLE 3. *Spaltung in F_2.*

Feldnummer	Kreuzung	Anzahl Pflanzen	Gefunden grün: *chlorina*	Erwartet (wahrscheinlichster Spaltungsmodus) grün: *chlorina*	P für verschiedene Spaltungsmodi: 3 : 1	15 : 1	63 : 1
1932—921 r 1	*chlorina* × Siegeshafer	625	590 : 35	585,9 : 39,1	—	> 0,30	—
1932—921 r 2	*chlorina* × Abeds Nova	229	184 : 45		> 0,05	< 0,01	—
r 3	»	83	68 : 15		> 0,10	< 0,01	—
r 4	»	246	175 : 71		> 0,10	< 0,01	—
r 5	»	87	74 : 13		> 0,02	< 0,01	—
r 6	»	10	8 : 2		> 0,70	> 0,05	—
r 7	»	487	382 : 105		> 0,05	< 0,01	—
Σ r 2 — r 7		1142	891 : 251	856,5 : 285,5	> 0,01	—	—
1932—921 r 8	*chlorina* × Glockenhafer II	449	439 : 10		—	< 0,01	> 0,20
r 9	»	279	272 : 7		—	< 0,02	> 0,20
r 10	»	1066	1034 : 32		—	< 0,01	< 0,01
r 11	»	37	37 : 0		—	> 0,10	> 0,30
r 12	»	730	722 : 8		—	< 0,01	> 0,20
r 13	»	999	972 : 27		—	< 0,01	< 0,01
r 14	»	118	117 : 1		—	< 0,02	> 0,50
Σ r 8 — r 14		3678	3593 : 85	3620,5 : 57,5	—	—	< 0,01
Σ r 8, 9, 11, 12, und 14		1613	1587 : 26	1578,8 : 25,2	—	—	> 0,80
1932—921 r 15	*chlorina* × Hedehafer	176	175 : 1		—	< 0,01	> 0,20
r 16	»	668	650 : 18		—	< 0,01	< 0,02
r 17	»	636	626 : 10		—	< 0,01	> 0,99
r 18	»	757	739 : 18		—	< 0,01	> 0,05
Σ r 15 — r 18		2237	2190 : 47	2202,0 : 35,0	—	—	> 0,02
1932—921 r 19	*chlorina* × 0101	441	322 : 119		> 0,30	< 0,01	—
r 20	»	732	556 : 176		> 0,50	< 0,01	—
r 21	»	888	683 : 205		> 0,10	< 0,01	—
r 22	»	942	714 : 228		> 0,50	< 0,01	—
Σ r 19 — r 22		3003	2275 : 728	2152,2 : 750,8	> 0,30	—	—

tungszahlen der verschiedenen Kreuzungen zum Teil von einander stark abweichen. Dies tritt noch deutlicher hervor, wenn die Spaltungszahlen grün : *chlorina* in Prozent angegeben werden wie in Tabelle 4.

TABELLE 4. *Spaltungszahlen für chlorina-Pflanzen in F_2, prozentisch ausgedrückt.*

Prozentsatz *chlorina*-Pflanzen beim Spaltungsmodus 3 : 1 = 25,0 %.
» » » » » 15 : 1 = 6,3 %.
» » » » » 63 : 1 = 1,6 %.

Feldnummer	Kreuzung	% *chlorina*	Feldnummer	Kreuzung	% *chlorina*
1932—921 r 1	*chlorina* × Siegeshafer	5,6	1932—921 r 12	*chlorina* × Glockenhafer II	1,1
			r 13	»	2,7
	chlorina × Abeds Nova-		r 14	»	0,8
r 2	Hafer	19,6			
r 3	»	18,1		*chlorina* ×	
r 4	»	28,9	r 15	Hedehafer	0,6
r 5	»	14,9	r 16	»	2,7
r 6	»	20,6	r 17	»	1,6
r 7	»	21,6	r 18	»	2,4
	chlorina ×			*chlorina* ×	
r 8	Glockenhafer II	2,2	r 19	0101	27,0
r 9	»	2,5	r 20	»	24,0
r 10	»	3,0	r 21	»	23,1
r 11	»	0,0	r 22	»	24,0

Es ist dann leicht zu konstatieren, dass dieses Zahlenverhältnis für die Kreuzungen mit Abeds Nova bzw. mit der Linie 0101 sich dem Verhältnis 3 : 1 nähert (25 % *chlorina*-Pflanzen), während in den Nachkommen von den Kreuzungen mit Glockenhafer II und dem Hedehafer eine viel grössere Anzahl von grünen Pflanzen vorkommt. Hier ist es wahrscheinlich, dass es sich um Spaltung nach 63 : 1 (1,6 % *chlorina*-Pflanzen) handelt. In F_2 von der Kreuzung mit Siegeshafer stimmt die Spaltungszahl mit dem Verhältnis 15 : 1 (6,3 % *chlorina*-Pflanzen) am besten überein.

Um die Übereinstimmung der erhaltenen Spaltungszahlen mit den erwähnten Zahlenverhältnissen näher festzustellen, wurden für jede Kreuzung die χ^2- und P-Werte ausgerechnet, und zwar nicht nur für das Zahlenverhältnis, welches wir nach der in Tabelle 4 gemachten

preliminären Berechnung als das Wahrscheinlichste gefunden haben, sondern auch für ein anderes Spaltungsalternativ, das hier eventuell auch in Frage kommen könnte. Diese so berechneten χ^2- und P-Werte sind in Tabelle 3 rechts eingetragen worden. Ein Vergleich zwischen diesen P-Werten für die verschiedenen, spaltenden F_2-Parzellen ergibt, dass für die Kreuzungen mit Abeds Novahafer und der Linie 0101 der Spaltungsmodus 3 : 1, für die mit Siegeshafer 15 : 1 und für die mit Glockenhafer II und Hedehafer 63 : 1 als höchstwahrscheinlich angesehen werden muss. Die F_2-Spaltungszahlen in den Kreuzungen mit 0101 und Siegeshafer dürften statistisch genügend gesichert sein, ohne dass hier auch eine F_3 gezogen werden müsste; dies gilt auch für die Kreuzung mit Abeds Novahafer, da die Wahrscheinlichkeit, dass hier das Verhältnis 15 : 1 anstatt 3 : 1 vorliege, als ausserordentlich gering betrachtet werden muss und demzufolge ausser Betracht fällt. Dagegen zeigte sich eine Nachprüfung in F_3 von den Kreuzungen mit Glockenhafer II und Hedehafer notwendig, da es hier gilt, eine Spaltung 63 : 1 sicher zu erkennen, wozu statistisch gesehen die Zahl spaltender Parzellen in F_2 allzu begrenzt ist. Es geht aus Tabelle 4 über die F_2-Spaltung hervor, dass in einigen Parzellen die Abweichungen vom erwarteten Spaltungsmodus recht beträchtlich sind. Bei den 3 : 1 und 15 : 1 spaltenden Kombinationen besteht die Abweichung regelmässig in einem Defizit an *chlorina*-Pflanzen gegenüber der Zahl theoretisch erwarteten. Dies wird durch die langsamere Keimungsenergie der *chlorina*-Form, ihre grössere Empfindlichkeit gegen z. B. Fritfliegenbefall und überhaupt allgemein ungünstigen Aussenbedingungen beim Aufgang erklärt, welche Erklärung durch die früher (siehe pp. 384—389) gemachten Erfahrungen in *chlorina*-spaltenden Beständen von Goldregenhafer I durchaus unterstützt wird. In den genannten Kreuzungen mit Glockenhafer II und Hedehafer dagegen, wo eine Spaltung 63 : 1 preliminär angenommen werden muss, findet man leicht aus Tabelle 3, dass in beiden Fällen ein Überschuss an *chlorina*-Rezessiven durchschnittlich gefunden worden ist, was nur durch den beschränkten Umfang der Zahl spaltender F_2-Parzellen erklärt werden kann. In der F_2 von *chlorina* × Glockenhafer II erhält man, wenn alle 7 Parzellen zusammengenommen werden, 3593 grüne auf 85 *chlorina* — theoretisch sollte man 3620,5 : 57,5 erwarten — also ein ganz beträchtlicher Überschuss an Rezessiven. Lässt man die Reihen 10 und 13 weg, gibt die Summierung dagegen 1587 : 26. Theoretisch nach 63 : 1 sollte hier 1578,8 : 25,2 erwartet werden, was eine auffallend gute Übereinstimmung bedeuten würde.

Aus den F_2 von den Kreuzungen mit Glockenhafer II und Hedehafer wurden F_3-Nachkommenschaften von normalgrün aussehenden Pflanzen gezogen. Dies geschah im Jahre 1935 in Erdkästchen während des Sommers. Die Bedingungen für die Entwicklung der *chlorina*-Pflanzen waren damit möglichst begünstigt, Fritfliegenbefall war ausgeschaltet, und für ein sehr gleichförmiges, optimales Keimbett mit angepasster Feuchtigkeit beim Aufgang war dadurch gesorgt. Nach Aufzählung der Spaltungszahlen wurde für jede spaltende Parzelle χ^2 und P für verschiedene alternative Spaltungsmodi berechnet. In der Übersicht unten in Tabelle 5 sind die derart als wahrscheinlich befundenen Spaltungszahlen nach dem Schema 63 : 1 eingeführt worden zugleich mit dem P-Wert der betreffenden 63 : 1-spaltenden Parzelle.

Die oben genannten in F_3 3 : 1- und 15 : 1-spaltenden Nachkommenschaften sind hier nicht aufgeführt worden; die prozentuelle Verteilung der in F_3 3 : 1-, 15 : 1- und 63 : 1-spaltenden Parzellen hat indessen durchaus die Erwartung bestätigt. Schon ein Blick auf Tabelle 5 genügt übrigens, um feststellen zu können, dass hier echte trimere Spaltung vorliegt.

DISKUSSION DER ERGEBNISSE.

Auf Basis dieser Befunde können wir also berechtigt sein, den Schluss zu ziehen, dass beim Kulturhafer drei polymere Faktoren vorkommen, welche je für sich die *chlorina*-Konstitution in normale Chlorophyllentwicklung verwandeln. Auch in heterozygoter Form vermag jeder dieser Faktoren (*Chlor 1*, *Chlor 2* und *Chlor 3*) normale Chlorophyllentwicklung hervorrufen. Volle Dominanz liegt also vor — dies im Gegensatz zu den drei einfaktorigen Heterozygoten bei der *lutescens*-Sippe, die während eines gewissen Entwicklungsstadiums gelbgefleckt sind und dann von den dominanten, einfaktorigen Homozygoten unterschieden werden können. Bei Goldregenhafer I, 0101 und Abeds Novahafer kommt ein solcher *Chlor*-Faktor vor, beim Siegeshafer zwei und beim Glockenhafer II und dem Hedehafer drei solche. Weitere Kreuzungen mit anderen Hafersorten sind vorgenommen, um eine Auffassung über die Zahl von *Chlor*-Faktoren bei verschiedenen Kulturhafersorten zu erhalten. Die *lutescens*-Sippe ist auch in dieser Hinsicht weiterbearbeitet worden.

Man kennt zurzeit beim Hafer äusserst vereinzelte Fälle von erblichen Variationen in der Chlorophylleigenschaft. Dies gilt auch für den Weizen (vgl. ÅKERMAN, 1922, S. 166). Beim Hafer beschränken

TABELLE 5. *63 : 1-spaltende Nachkommenschaften in F_3 von den Kreuzungen chlorina × Glockenhafer II und Hedehafer.*

Herkunft in F_2	Feldnummer in F_3	Kreuzung	Anzahl Pflanzen	Gefunden grün : *chlorina*	Erwartet nach 63 : 1 grün : *chlorina*	P für 63 : 1
1932—		*chlorina*				
921 r 8	1935-K- r 8	× Glock-	123	121 : 2	121,05 : 1,95	> 0,95
	r 14	enhafer	91	90 : 1	89,6 : 1,4	> 0,20
	r 24	II	90	88 : 2	89,6 : 1,4	> 0,20
	r 25		93	91 : 2	91,5 : 1,5	> 0,80
	r 58		77	75 : 2	75,8 : 1,2	> 0,30
	r 61		39	38 : 1	38,4 : 0,6	> 0,50
	r 79		110	107 : 3	108,3 : 1,7	> 0,30
	r 84		79	78 : 1	77,7 : 1,3	> 0,70
	r 89		69	68 : 1	67,905 : 1,095	> 0,95
	r 92		73	72 : 1	71,9 : 1,1	> 0,70
	r 100		101	100 : 1	99,4 : 1,6	> 0,50
	r 103		47	46 : 1	46,3 : 0,7	> 0,90
	r 107		37	36 : 1	36,4 : 0,6	> 0,50
	r 132		123	122 : 1	121,1 : 1,9	> 0,50
	r 138		139	137 : 2	136,8 : 2,2	> 0,90
	r 143		104	101 : 3	102,4 : 1,6	> 0,20
	r 144		42	41 : 1	41,3 : 0,7	> 0,70
	r 146		123	122 : 1	121,1 : 1,9	> 0,50
	r 170		44	43 : 1	43,3 : 0,7	> 0,90
1932—	1935-K-	*chlorina*				
921 r 10	r 202	× Glock-	133	132 : 1	130,9 : 2,1	> 0,30
	r 203	enhafer	130	127 : 3	128,0 : 2,0	> 0,30
	r 210	II	113	111 : 2	111,2 : 1,8	> 0,70
	r 216		104	102 : 2	102,4 : 1,6	> 0,70
	r 228		62	61 : 1	60,02 : 0,98	> 0,95
	r 232		76	75 : 1	74,8 : 1,2	> 0,80
	r 242		72	71 : 1	70,9 : 1,1	> 0,95
	r 252		63	61 : 2	62,02 : 0,98	> 0,20
	r 259		109	106 : 3	107,3 : 1,7	> 0,30
	r 264		133	130 : 3	130,9 : 2,1	> 0,50
	r 299		80	78 : 2	78,7 : 1,3	> 0,50
	r 324		53	52 : 1	52,2 : 0,8	> 0,90
1932—	1935-H-	*chlorina*				
921 r 16	r 20	× Hede-	118	116 : 2	116,2 : 1,8	> 0,80
	r 22	hafer	73	71 : 2	71,9 : 1,1	> 0,30
	r 25		132	130 : 2	129,9 : 2,1	> 0,90
	r 28		126	122 : 4	124,04 : 1,96	> 0,10
	r 32		66	65 : 1	64,99 : 1,01	> 0,95

Herkunft in F_2	Feldnummer in F_3	Kreuzung	Anzahl Pflanzen	Gefunden grün: *chlorina*	Erwartet nach 63 : 1 grün: *chlorina*	P für 63 : 1
	r 39		65	64 : 1	63,97 : 1,03	> 0,95
	r 47		123	120 : 3	121,1 : 1,9	> 0,30
	r 53		42	41 : 1	41,3 : 0,7	> 0,70
	r 55		48	47 : 1	46,5 : 1,5	> 0,70
	r 87		137	134 : 3	134,9 : 2,1	> 0,50
	r 94		65	63 : 2	64 : 1	> 0,30
	r 95		111	109 : 2	109,3 : 1,7	> 0,80
	r 109		70	68 : 2	68,9 : 1,1	> 0,30
	r 115		134	132 : 2	131,9 : 2,1	> 0,90
	r 120		51	50 : 1	50,2 : 0,8	> 0,80
	r 122		119	118 : 1	117,1 : 1,9	> 0,30
	r 128		136	132 : 4	133,9 : 2,1	> 0,10
	r 130		135	132 : 3	132,9 : 2,1	> 0,50
	r 136		76	75 : 1	74,8 : 1,2	> 0,80
	r 139		96	95 : 1	94,5 : 1,5	> 0,70
	r 144		114	113 : 1	112,2 : 1,8	> 0,50
	r 151		103	102 : 1	101,4 : 1,6	> 0,50

sich die bisher genauer genetisch analysierten Fälle von polymer bedingten Chlorophylleigenschaften in der Tat — unseres Wissens — zu der *lutescens*-Sippe und der hier erwähnten *chlorina*-Form. In beiden Fällen scheinen nicht mehr als drei polymere Gene an der Spaltung beteiligt zu sein.

Augenscheinlich dürften wohl die *lutescens*- sowie die *chlorina*-Sippe mit ihrem — wahrscheinlich durch Reduplikation ein und desselben Gens — trimer bedingten Erbgang als typische Beispiele von Polymerie infolge Polyploidie sein. Sämtliche hier untersuchten Hafersorten sind hexaploid.

Dieser Spezialfall innerhalb des klassischen Polymeriebegriffes von LANG (1911) ist in der späteren Diskussion von TJEBBES (1931) vorschlagsweise als »homomerism» bezeichnet worden, obwohl, wie er selbst schreibt, PLATE (1913) den Begriff »Homomerie» als identisch mit Polymerie in dem ursprünglichen Umfang verwendet hat. NILSSON-EHLE (1915) setzt auch zwischen »Polymerie» und »Homomerie» vollkommene Identität. Der durchaus gute Gedanke von TJEBBES, dem schon geprägten Begriff »Homomerie» einen spezielleren Inhalt zu geben, scheiterte und verursachte eine gewisse Verworrenheit, die noch zu bestehen scheint. Aus Prioritätsgründen dürfte daher TJEBBES' Vorschlag: . . . »the occurrence of one and the same gene in duplicate

or triplicate condition might be called homomerism» (TJEBBES, 1931, S. 253) abgelehnt werden müssen. Man könnte dann z. B. entweder von »Polymerie infolge Polyploidie» oder nach einem Vorschlag von O. TEDIN, von *homologen*, polymeren Faktoren sprechen. Dabei behält man den Grundbegriff intakt und vermeidet ein Missverständnis.

Wenn man bedenkt, welche äusserst umfangreiche Areale in Form von Haferparzellen jedes Jahr bei den Svalöfer Züchtungsarbeiten durchmustert werden, fällt sofort auf, dass die in dem einfaktorigen Goldregenhafer I im Jahre 1925 in einer Gamete aufgetretene, mutative Veränderung zu dem heterozygoten Zustand die *einzige beobachtete* während einer Zeit von mehr als 25 Jahren ist! In den ebenfalls als einfaktorig (*Chlor 1 Chlor 1 chlor 2 chlor 2 chlor 3 chlor 3*) befundenen Hafersorten 0101 und Abeds Nova ist dieselbe Veränderung (zu *Chlor 1 chlor 1* . . . .) noch *nie* aufgefunden worden — die Linie 0101 und der Abeds Novahafer laufen jedoch in konstant zu betrachtender Form ebenfalls seit einer langen Zeit in den Svalöfer Feldversuchen. Während dieser Zeit sind alle Parzellen sorgfältig auf abweichende Formen untersucht worden — in erster Linie hätte man dann die verhältnismässig leicht zu entdeckenden chlorophyllaberranten Formen, falls solche aufgetreten wären, mit sehr grosser Wahrscheinlichkeit finden müssen. Es muss daher von diesen Tatsachen der Schluss gezogen werden, dass die spontane Mutationsfrequenz im einfachen Faktorspaare äusserst gering ist. Es ist dann natürlich kein Wunder, dass bei dem bezüglich der *chlorina*-Eigenschaft zweifaktorigen Siegeshafer keine rezessiven Homozygoten im Laufe der letzten drei Jahrzehnte ausgespaltet worden sind. Wenn die gleiche, sehr geringe Mutationsfrequenz in beiden Faktorspaaren vorausgesetzt wird, vermindern sich die Aussichten ungeheuer, dass eine doppeltheterozygote Pflanze *Chlor 1 chlor 1 Chlor 2 chlor 2* auftreten könnte, die in der nächsten Generation 15 : 1 spaltet. Es braucht schliesslich kaum erwähnt zu werden, welch' praktisch unendlich kleine Aussichten bestehen, eine *chlorina*-Ausspaltung aus dreifaktorigen Hafersorten (z. B. Glocken II und Hedehafer) zu erhalten, weil sich ja hier der Mutationsvorgang in sämtlichen drei Faktorspaaren abspielen muss.

Die von ÅKERMAN untersuchte *lutescens*-Sippe trat zwar nicht als Mutation aus einer einfaktorigen Hafersorte auf, sondern entstand aus der Kreuzung zwischen dem betreffs der *lutescens*-Eigenschaft nunmehr (ÅKERMAN, 1929) als zweifaktorig befundenen Abeds Novahafer (L_pL_p L_nL_n l_sl_s) und dem nun als einfaktorig klassifizierten Schwarzhafer Glocken II (l_pl_p l_nl_n L_sL_s). Aus dieser Kreuzung spalteten *lutescens*-

Pflanzen nach 63 : 1 aus; der Faktor bei Glockenhafer II war also mit keinem der Abeds Nova-Faktoren identisch. Nun sind aber in Svalöf weder bei Glockenhafer II noch bei anderen, einfaktorigen Schwarzhafersorten *lutescens*-Pflanzen spontan-mutativ je gefunden worden! Auch in diesem Falle von einem polymer bedingten Chlorophylldefekten müssen wir also eine ausserordentlich geringe spontane Mutationsfrequenz erschliessen.

Das ausserordentlich stark beschränkte spontane Vorkommen von faktoriell mendelnden Chlorophyllaberrationen beim Hafer und Weizen ist schon mehrmals von ÅKERMAN (1922, 1929; ÅKERMAN und MÜHLOW, 1933) hervorgehoben worden, dies als ein Gegensatz zu den Verhältnissen bei der diploiden Gerste und der ebenfalls diploiden Erbse, wo bekanntlich spontane, letale oder subletale Chlorophyllaberrationen bedeutend öfter auftreten. Auch beim Mais, Löwenmaul u. a. genauer erforschten Diploiden sind spontane Mutationen, die die Chlorophyllentwicklung eingreifend stören, in nicht geringer Zahl bekannt. Ehe die *lutescens*- bzw. *chlorina*-Sippen noch entdeckt waren, kannte man beim Hafer — ausser Komplexmutationen vom Fatuoidtypus — nur Mutationen in der Kornfarbe von schwarz zu grau- oder weisskörnigen Typen. NILSSON-EHLE zeigte (1911), dass diese grau- oder weisskörnigen Pflanzen nicht das Resultat von Kreuzungen sein konnten, sondern dass ihre Entstehung einwandfrei mutativ geschehen sein musste. Spätere, umfassendere Untersuchungen in der Kontrollabteilung des Saatzuchtvereines ergaben, dass die Mutationsfrequenz der allgemein angebauten Schwarzhafersorten Engelbrekt II und Stormogul II so hoch als 1 : 2000 war. Es müssen daher jährlich kostspielige Reinigungsmassnahmen unternommen werden, um diese Schwarzhafersorten rein zu erhalten. Man strebt deshalb nunmehr danach, Sorten mit zwei polymeren Schwarzfaktoren zu züchten. Mit einer Mutationsfrequenz von 1 weissen oder grauen Korn auf 2000 schwarze hat man bei einer zweifaktorigen Sorte, die gleiche Mutationsfrequenz in beiden Faktorspaaren vorausgesetzt, nur eine Frequenz von $1/2000 \times 1/2000 = = 1/4000000$ zu erwarten, d. h. in 132 Kg. Schwarzhafer-Saatgut nur ein weisses Korn. Eine solche Hafersorte ist Svalöfs Orionhafer II, die auch erwartungsgemäss praktisch keine weissen Körner gibt.

Die verhältnismässig hohe Mutationsfrequenz des Schwarzhafers in bezug auf Kornfarbe führte dazu, als Ursache des Fehlens von Chlorophyllmutationen bei Hafer polymere Bedingtheit der Chlorophylleigenschaft »normale Chlorophyllausbildung» anzunehmen und zwar nach KIHARAS Feststellung, dass der Hafer ein Hexaploid ist

(KIHARA, 1919), derart ausgeformt, dass typische »Polymerie infolge Polyploidie» oder »homologe, polymere Faktoren» hier als Erklärung vorgeführt wurden. Obwohl auch bei Diploiden polymere Chlorophyllfaktoren (im weiteren Sinne) gefunden worden sind, z. B. bei *Zea Mays* (DEMEREC and EMERSON, 1924—25), kann man indessen ohne weiteres feststellen, dass die weitaus überragende Zahl bisher gefundener Chlorophyllaberrationen bei Diploiden monomer erbbedingt sind. Daher ist die Hypothese, dass man in Auto- wie auch Allopolyploiden wirklich mit reduplizierten, identischen Faktorspaaren zu tun hat, nicht unwahrscheinlich. Die Einwendung, dass bei Allopolyploiden die verschiedene Herkunft der Genome die Reduplikationshypothese stark schwächt, muss abgelehnt werden. Denn gerade die lebenswichtigen Gene, die der normalen Chlorophyllentwicklung zugrunde liegen, dürften kaum auch den Genomen mit entfernterer Verwandtschaft fehlen. Man darf übrigens nicht vergessen, wie von MÜNTZING (1936, S. 366) hervorgehoben wird, dass die Übereinstimmung zwischen Allo- und Autopolyploiden grösser ist als die Verschiedenheiten, dies auf Grund der Tatsache, dass alle Allopolyploide teilweise autopolyploid sind.

Die Auffassung von einem Zusammenhang zwischen homologen, polymeren Faktoren und tetraploider bzw. hexaploider Konstitution ist mehrmals zur Diskussion aufgeworfen worden. Sie wird u. a. von MÜNTZING im Zusammenhang mit der Feststellung dimeren Erbgangs für Haarigkeit in *Galeopsis Tetrahit* (tetraploid!) ausgesprochen (MÜNTZING, 1937, S. 397—398). Bei der Erinnerung daran, dass die ausgeprägtesten Fälle von Polymerie in polyploiden Arten gefunden worden sind (NILSSON-EHLE, 1909; ÅKERMAN, 1922; MEURMAN, 1926; ÅKERMAN und MÜHLOW, 1933; J. CLAUSEN in *Viola*, 1931) findet MÜNTZING, »that it is certainly not a simple occurrence that the most typical cases of polymeric factors have been found in polyploid species».

Wenn beim Hafer durch das oben Angeführte das Vorkommen reduplizierter Gene für die Kornfarbe und nunmehr auch gewisse letale oder subletale Chlorophyllaberrationen wahrscheinlich gemacht worden ist, kann man trotzdem das Problem der Seltenheit von Chlorophyllaberrationen bei dieser Getreideart nicht als endgültig erläutert betrachten. Es wurde schon oben ausführlich über die ausserordentlich geringe Mutationsfrequenz der einfaktorigen Hafersorten berichtet — nur die *chlorina*-Sippe entstand übrigens rein mutativ. Im Vergleich mit der hohen Frequenz der Kornfarbenmutationen und auch mit der der Fatuoidmutationen (obwohl sie wahrscheinlich einer ganz

anderen Art von Mutationen angehören), ist es noch eine offene Frage, warum die einfaktorigen Hafersorten in bezug auf sowohl *chlorina*- wie *lutescens*-Mutationen — wie auch auf noch nicht entdeckte Mutationstypen — eine so ungeheuer niedrige Mutationsfrequenz haben. Eingehende, längst laufende Röntgenbehandlungen von verschiedenen Hafersorten und -Arten (FRÖIER, 1941; vorläufige Mitteilung) werden wahrscheinlich im Zusammenhang mit zytogenetischen Untersuchungen über die genomatische Stabilität der tetra- und hexaploiden Hafertypen im Vergleich mit der der diploiden Formen weiteres Licht über diese noch sehr unklaren Verhältnisse werfen können.

SUMMARY.

The title of the paper is: Studies on a spontaneous *chlorina* mutation in *Avena sativa*.

An account is given of the spontaneous appearance of a new, chlorophyll-deficient, sublethal, recessive oat mutation, f. *chlorina*. This new strain has been briefly mentioned previously by ÅKERMAN (1929; ÅKERMAN and MÜHLOW, 1933), but so far a more detailed account has not been given. The *chlorina* plants are yellowish-green, and although retarded in development as compared with normal plants, reach maturity and can be propagated by their own seeds. The mother strain, in which ÅKERMAN in 1928 discovered this mutation, was Svalöf's Guldregn I (Golden Rain I), an old pedigree selection from Milton oats (a Probsteier variety).

The segregation in the subsequent generations (Tables 1—2) shows the monofactorial constitution of the variety Guldregn I in respect to the *chlorina* character. The influence of environmental factors in general and especially of attacks of frit fly (*Oscinella frit* L.) on the expected segregation ratios in certain years is discussed.

Some physiological data, obtained in the course of the study of the *chlorina* plants, suggest that the plant-weight of the recessive form, already at a rather early stage of development, is inferior to that of the normal green plant (Fig. 1), this difference being still more accentuated in the further stages of development. Physiological researches concerning assimilation and respiration intensity are at present being carried out in order to increase our knowledge of the action of a typical, isolated »single chlorophyll factor». This is being done because there is hardly any case where such a single factor action

could be better studied as in the case of a monofactorial mutation, segregating in mother form and mutant.

Systematic crosses have been started in order to determine if more than one factor in cultivated oats was responsible for the manifestation of the *chlorina* constitution. At present five oat strains have been thoroughly investigated. F_2 (Table 3) revealed the most probable existence of three polymeric factors (*Chlor 1*, *Chlor 2*, *Chlor 3*), and F_3 (Table 5), finally, gave full statistical evidence of the segregation 63 green : 1 *chlorina*. The dominance of each factor for normal chlorophyll development is obviously complete. Each of the three possible monofactorial heterozygotes (*Chlor 1 chlor 1*, *Chlor 2 chlor 2*, etc.) is normal green in all developmental stages. This report thus offers the second known case of trifactorial polymeric chlorophyll inheritance in hexaploid oats. The first case was the f. *lutescens* (ÅKERMAN, 1922). Abed's Nova oats and the strain 0101 have one *Chlor*-factor, Svalöf's Segerhavre (Victory) two. Svalöf's Klockhavre II (Bell II) and Hede oats (old land-variety of Danish origin) possess each three. The systematical crosses are continued on a large scale in order to obtain a statistical idea of the distribution of homologous, polymeric factors in oats.

The correct use of the terms »polymeric» and »homomeric» factors is briefly discussed. The historical priority of the term »polymerism» (LANG, 1911) in its broad, primary sense is stressed, this term being identical with »homomerism» (PLATE, 1913; NILSSON-EHLE, 1913 [published 1915]). TJEBBES (1931) suggested that »homomerism» should be limited to »polymerism caused by polyploidy», *i. e.* reduplication of identical factors. This suggestion, however, failed to gain acceptance, but has caused and still causes misunderstandings. In order to avoid misinterpretations, Dr. O. TEDIN, Svalöf, has suggested to the present authors the term »homologous, polymeric factors» for a polyploid reduplication of identical factors, which suggestion the authors fully adopt.

In the last part of the paper the exceedingly low frequency of the very rare spontaneous chlorophyll mutations known in oats and wheat is discussed. Since factors occur — especially in oats — which mutate spontaneously as frequently as 1 : 2000 (black kernels to grey or white kernels), the existence of homologous, polymeric factors cannot be the only cause of the extremely rare chlorophyll mutating processes in these hexaploids. In the case of f. *lutescens* (ÅKERMAN, l. c.) as well as of f. *chlorina* the existence of monofactorial commercial oat strains

has been shown. And yet their spontaneous chlorophyll mutation rate is nil or practically nil, which has been confirmed at Svalöf during the past two decades or more. X-ray experiments are being carried out in order to study the appearance and frequency of new, induced mutations and thus to obtain further knowledge of the stability of the chlorophyll apparatus in different polyploid oats.

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